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THE CONDOR

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THE CONDOR

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

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THE CONDOR

VOLUME 63 JULY-AUGUST, 1961 NUMBER 4

AVIAN DAYBREAK AND EVENING SONG IN RELATION TO TIME AND LIGHT INTENSITY

By Aldo Leopold and Alfred E. Eynon

This paper reports an attempt to measure the variation in the time and the light intensity at the onset and at the end of daily bird song as recorded in southern Wisconsin, principally in the years 1944 through 1947. The first songs of birds at daybreak or their last songs at evening have been the subject of numerous papers in both American and European ornithological literature. The usual approach has been to construct an "ornithological clock" based on the order in which species join or leave the morning or evening chorus, respectively, or to relate such songs to some standard time-marker such as sunrise, sunset, or civil twilight. In America, at least, there has been a paucity of data on the light intensity at the time when these phenomena occur. Such data are reported here for 20 species of North American birds.

The field work on which this paper is based was done by the senior author whose death on April 21, 1948, brought to an end a study of bird song in which he had become increasingly absorbed during the last years of his life. The junior author's role has been to analyze Professor Leopold's abundant data as they were recorded in his charts and journals and to organize them for publication. Fortunately, there exists an unpublished manuscript by Leopold, written after the song season of 1944 and covering wider horizons, which expresses his thinking regarding much of the subject matter of this paper. This manuscript has been freely consulted and the discussion therein amplified or modified following an analysis of Leopold's field records for the years 1945 through 1947. The junior author has introduced certain ideas derived from his interpretation of the data, combined with a review of the expanding literature appearing after 1947.

The season of bird song *per se* will not be discussed because Leopold's data on that subject were published by Zimmerman (1951).

In this study, observations were made in a suburban habitat on the west side of Madison, Wisconsin (latitude 43° 4′ N, longitude 89° 24′ W), and on an abandoned farm 34 miles to the northwest in Fairfield Township, Sauk County. These study areas are referred to as town and farm, respectively, in this paper. They differ from one another by about one minute in their time of sunrise at the June solstice. Observations in the two study areas made possible the inclusion of more species than could be found at either area alone and at the same time allowed more or less daily observation of species common to both areas. The record for species not common to both is naturally discontinuous, but this is offset to some extent by the inclusion of data for several years.

The principal records were obtained between January 8, 1944, and April 20, 1948. Over these years observations were recorded on 804 mornings and 164 evenings (table 1). Of the 804 observations at daybreak, 445 fall in the period between January 8, 1944, and June 30, 1945. No attempt was made to obtain a daily record after the waning of the song season in 1945. The research emphasis then simply shifted to a sampling process in which many photometric data were accumulated.

For each species on a given day, "daybreak song" is the initial song of the day and occurs not later than one hour after the first song of the day by any of the species heard

at the study areas. The term daybreak song is preferred to "awakening song" as used by Wright (1912 and 1913), Allen (1913) and Nice (1943) because some birds are awake for a time before they sing. Armstrong (1955) found that the interval between awakening and the first song of the European Wren (*Troglodytes troglodytes*) seldom exceeded a minute, but Scheer (1951) found that it averaged 3 minutes in the European Robin (*Erithacus rubecula*), 5 to 6 minutes in the European Blackbird (*Turdus merula*), and 15 to 20 minutes in the Chaffinch (*Fringilla coelebs*). We agree with Allard (1930) and Davis (1958) that the term "awakening song" is inadequate, but we imply synonymy with those authors who have also been concerned with the first song of the day.

TABLE 1

DISTRIBUTION OF MORNING AND EVENING OBSERVATION PERIODS

Month	Morning	Evening	Month	Morning	Evening
January	83	....	July	57	33
February	72	....	August	52	20
March	119	12	September	42	11
April	85	35	October	54	2
May	68	29	November	52	....
June	62	22	December	58	....

Similarly, "evening song" is the last song of the day and it occurs within the hour preceding the last song at evening by any of the species present. "Daytime song" is one falling between the two previously defined observation periods and will not be considered to any extent in this paper. True "night song" is that falling between the end of astronomical twilight in the evening and its beginning in the morning (Allard, 1930), and it was not recorded for any diurnal species during this study. However, birds sang occasionally as much as an hour before the beginning of civil twilight in the morning.

ACKNOWLEDGMENTS

We are indebted to J. T. Emlen, Jr., J. J. Hickey, R. A. McCabe, J. C. Neess, and many other colleagues at the University of Wisconsin for advice throughout the course of this study, as well as to J. P. Ditchman of the General Electric Company, Mrs. Georg Scheer, and H. A. Hochbaum.

METHODS

Prior to 1944, Leopold recorded the times of evening song and daybreak song for a number of common birds in which he was interested. His systematic timing of all species at both town and farm study areas began in 1944.

After early 1945, a General Electric foot-candle meter was used in most daybreak or evening observation periods. This instrument is calibrated on a primary scale of from 1.2 foot-candles to 50 foot-candles; however, this scale may be increased by means of a rheostat to read twice these values, or the values may be decreased by factors of 10 and 100. The range of possible values thus runs from 0.012 foot-candle to 100 foot-candles. Leopold read the meter in a standard manner, holding it horizontally on his lap, against open sky.

The record for each daybreak or evening observation period consists of the time and light intensity of the first or last song of each species, as well as remarks on relative cloudiness, wind, temperature, and moonlight if present. In February and most of March, when only the Cardinal (*Richmondena cardinalis*) and Ring-necked Pheasant (*Phasi-*

anus colchicus) are singing in southern Wisconsin, observations are possible from an open window, provided an active territory is near. All later observations require the observer to be outdoors in order to record distant or faint songs.

In May and June the babel of voices, especially at daybreak, makes only the earliest and loudest songs audible at any distance. Hence, a standard observation post was used at this season. In July and August the bedlam has ceased, the number of species singing has greatly declined, and distant recordings again become feasible. A circuit of several hundred yards was then used in order to cover several habitats.

No special problem attended the recording of daybreak song; time and light intensity were entered as each successive species began to sing. For cessation in the evening, a list of singing species was written in advance, and the values for each were then recorded every 5 minutes until all song had ceased. Terminal dates in phenology are usually cruder than beginning dates (Leopold and Jones, 1947). Since one never knows which song may be the last one of the day, we can only say that this yardstick applies equally well to evening song, especially when several species are being studied simultaneously.

In lumping days that Leopold entered on the original data sheets as clear with those entered as partly cloudy, we are supported by Scheer (1952), who found that a cloud cover of from $\frac{1}{10}$ to $\frac{3}{10}$ gave higher light-intensity values than a clear sky. Indeed, he found little difference in his curves of total illumination up to $\frac{7}{10}$ cloud cover, but cloudiness beyond this produced lower values.

GENERAL PATTERN OF DAYBREAK SONG

Stability of daybreak song.—In 1944 and 1945, Leopold obtained a close approach to a daily record of the time of first daybreak song for five breeding species: Mourning Dove (*Zenaidura macroura*), House Wren (*Troglodytes aedon*), Catbird (*Dumetella carolinensis*), American Robin (*Turdus migratorius*), and Cardinal. This record includes data from both study areas. Leopold's notes indicate that his estimate of the number of territories on which males were audible in 1944 (table 2) was largely unchanged in 1945 except for the Robin, when the small lawn and garden at the farm did not attract their usual single pair, and only song by very distant Robins was audible there. There is an annual "tuning-up" period in each of these species during which song occurs, but not daily, and often not at daybreak. The full-song period begins when song becomes regular at daybreak and remains so until daybreak song becomes irregular again in July or August at our latitude.

TABLE 2

NUMBER OF TERRITORIAL MALES AUDIBLE AT THE STUDY AREAS IN 1944

Species	Town	Farm
Mourning Dove	5	5
House Wren	3	4
Catbird	2	2
Robin	10	1
Cardinal	2	2

Careful studies of marked birds have shown that the song season is subject to interruptions and fluctuations. For many passerines, temporary cessation of song by individual males at the initial stage of pair formation has been reported by numerous authors. In the Song Sparrow (*Melospiza melodia*), song is irregular while adults are feeding young (Nice, 1943), and cessation occurs between broods in some double-brooded species (R. A. McCabe, *in litt.*). All but sporadic song ceases in most passerines while they are

molting. The composite record of daybreak song in a species population therefore will differ from that of an individual, depending on the number of territories and the degree of synchrony in the nesting cycle. A nonsynchronized population of many territorial males would probably show longer duration and fewer mornings without daybreak song than would an individual male. Stoddard (1931) and Davis (1958) found that the unmated males in a population are the most persistent singers in the Bobwhite (*Colinus virginianus*) and Rufous-sided Towhee (*Pipilo erythrophthalmus*), and such persistence is probably common in other species as well. The isolated mated male Robin at the farm in 1944 sang hardly at all.

The five species differed in the proportion of daybreaks in which song failed to be recorded. In table 3, only the full-song period and the daybreaks when song failure was positively recorded are considered. To determine which failures are traceable to weather,

TABLE 3

COMPARISON OF FAILURE OF DAYBREAK SONG IN 1944 AND 1945

Species	Year	Full song period	No. days	Days not recording	Days of failure	Failure traceable to weather	Per cent not due to weather
Cardinal	1944	Feb. 26 to June 22	118	22	10	4	6
	1945	Feb. 28 to July 5	128	23	25	2	22
Robin	1944	Mar. 25 to Aug. 3	132	15	8	2	5
	1945	Mar. 13 to July 17	127	25	4	3	1
Mourning Dove	1944	Apr. 1 to Aug. 21	142	12	4	1	2
	1945	Mar. 27 to Aug. 23	150	42	15	11	4
House Wren	1944	May 2 to Aug. 7	98	3	2	1	1
	1945	Apr. 25 to Aug. 13	111	30	2	1	1
Catbird	1944	May 12 to July 24	74	6	2	2	0
	1945	May 13 to July 13	62	21	2	1	2

we considered only heavy rain or strong wind to be sufficient grounds except that, in the Cardinal, we evaluated heavy snowfall at daybreak in February and early March. It is a matter of common observation that heavy rain inhibits bird song at any time of day. Many authors have stressed the importance of wind strength in delaying or inhibiting daybreak song, and Scheer (1952) found that it was the only weather factor which yielded a significant correlation in his analysis of the early morning song of the European Blackbird.

If we consider the Mourning Dove, Robin, and Cardinal during the periods of the 2 years in which all three species were in full song, there was not a single morning on which at least one failed to sing. Of the 40 dawns on which one of these three species failed to sing, two of the others sang on 33 mornings. The Robin sang at every daybreak on which the Mourning Dove failed to sing, and only once did the failure of the Robin to sing coincide with the failure of the Cardinal. There were five mutual failures by the Mourning Dove and the Cardinal in 1945, but only one in 1944.

Before the other two species began to sing regularly, however, the Cardinal failed to sing on 12 mornings in March, 1945. There were no Cardinal failures in March, 1944, despite the fact that it was colder and there was more snow than in 1945. A peculiar failure occurred on May 9, 1944. One bird sang at 3 a.m. in darkness, but no Cardinal song occurred at daybreak an hour later. There was no change in the weather.

Occasionally, failures were grouped in a suggestive manner. Robin song failed on successive days, May 21 and 22, 1944, in cloudy but calm weather, and first broods were

seen to fledge on these days. To impute a causal relationship, however, implies an improbable degree of nesting synchrony among at least 10 pairs.

Our data for evening song are insufficient to warrant any conclusions regarding its stability.

Fluctuations.—The time of daybreak song is a response to the stimulus of a certain light intensity which, within narrow limits, is characteristic of the species, although subject to individual variation. Among early European investigators to recognize this, according to Scheer (1952), were Haecker (1916) and Schwan (1921–22). In America the early emphasis was on the time at which birds first sang in the morning (Wright, 1912, 1913; Allen, 1913) with little regard for some standard measure of equal light intensity and less regard for different latitudes and changing seasons. Craig (1926) was

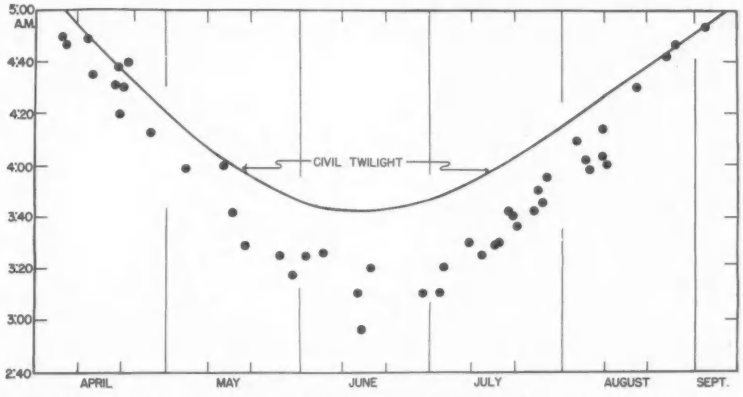

Fig. 1. Earliest daybreak song of the Field Sparrow (*Spizella pusilla*) on clear to partly cloudy mornings in relation to the beginning of civil twilight at the farm, 1944 to 1947.

the first to use the curve of the beginning of civil twilight in relation to the song of the Eastern Wood Pewee (*Contopus virens*), and Allard (1930) published a series of such curves. The latter were combined in a figure that clearly showed the limitations of the "ornithological clock," but he smoothed his curves mathematically by the method of least squares. This method seems to us to have a basic defect: it depicts the weather as well as the bird. To depict the bird alone, it seems preferable to plot the daybreak songs for clear or partly cloudy mornings and to note the fluctuations in relation to the beginning of civil twilight (figs. 1, 2).

The Field Sparrow (*Spizella pusilla*) had a daybreak song that showed a minimum amount of irregularity (fig. 1). We mean by this that, if a curve of best fit were to be drawn through the dots which indicate the earliest songs, it would be relatively close to all of them and would form a symmetrical arc with the greatest departure from the civil twilight curve corresponding very well to the earliest occurrence of that standard measure. The very early record for this species fell on June 15, 1944, at 2:56 a.m. with a clear moon at last quarter.

The Catbird, on the other hand, exhibited a maximum amount of irregularity (fig. 2). The song began very close to civil twilight in the second week of May, but then a wide scatter of readings followed, with the earliest songs occurring well before the solstice.

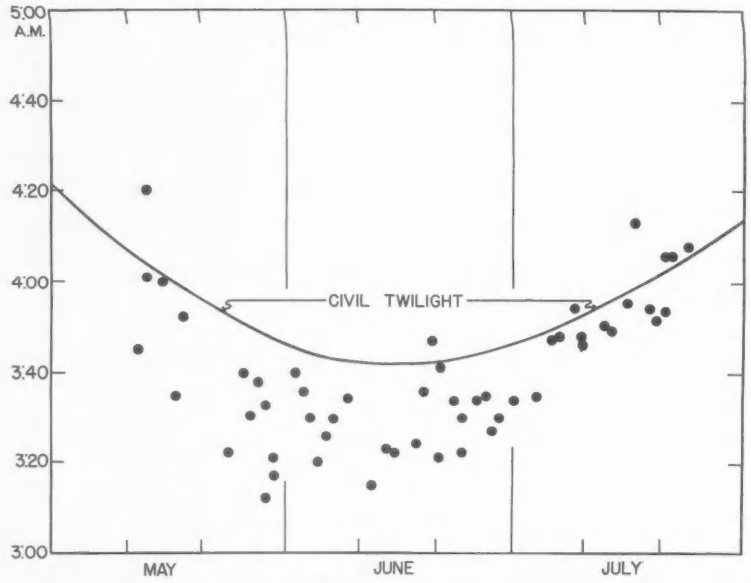

Fig. 2. Earliest daybreak song of the Catbird (*Dumetella carolinensis*) in relation to the beginning of civil twilight on clear or partly cloudy mornings only, 1944 to 1947. Data from both study areas are included.

After early June, daybreak song of the Catbird became later and displayed a gradual angle to the civil twilight curve, which it crossed in the third week in July. Curves for Catbirds for the individual years 1944 and 1945 on file in the Department of Forestry and Wildlife Management, University of Wisconsin, reveal that this irregularity is not an artifact of composite data.

Leopold's data are most complete for the Cardinal. These are presented in a somewhat different form (fig. 3) because the records are so numerous, and because this bird may sing at any time throughout the year. Song is rare, however, between the end of August and late December. Despite this annual hiatus, the time of daybreak song was recorded on 345 days during this study. Means for 3– day periods have been indicated when at least three records for such intervals are available and include daybreak song heard under all weather conditions. These means, we feel, are good indicators of when the daybreak song of Cardinals may usually be heard throughout the year. Some of the means are computed for as many as 12 observations. The earliest songs heard under clear skies have been added to indicate the normal song curve when conditions are ideal. These clear-sky records compare to the curves given previously for the Field Sparrow and the Catbird.

The Cardinal, if unhampered by weather, sang after the beginning of civil twilight from late December until about mid-March. By April 1, the daybreak song came well ahead of civil twilight, but the interval did not increase for a month. Two periods of irregularity are evident in the means and in the earliest records in early May and at the solstice. These periods are evident on the single-year curves as well, so that what is

shown here in composite form is a fair representation of what happened each year of the study.

The House Wren appeared to have as little or less irregularity than the Field Sparrow, but when the audible males at town and farm are analyzed as separate groups (fig. 4), the two populations are seen to begin singing at consistently different times. At the farm, these wrens gave the daybreak song ahead of civil twilight on all occasions except the initial song and during tapering-off periods at the end of the song season. However, daybreak song in town was rarely heard before civil twilight began. The reason for exclusion of the year 1947 from the curve for the House Wren is simple: there were no audible males at the town observation post.

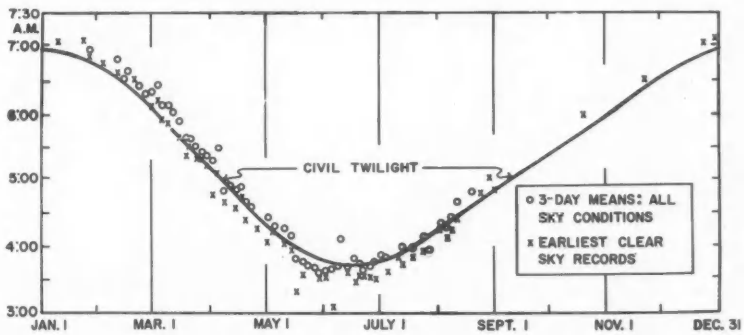

Fig. 3. Daybreak song of the Cardinal (*Richmondena cardinalis*), February 26, 1944, through April 20, 1948, in relation to the beginning of civil twilight; curve is based on 345 daybreak songs and includes both study areas. (See text for additional details.)

Allard (1930), who was able to observe two House Wrens with known roosting places, found one consistently singing earlier than the other. Armstrong (1955) found a similar difference between two European Wrens which amounted to about 10 minutes. Both of these observations involved birds at a single locality, and the variation could be attributed to a difference in exposure of the roosting site to the dawn light, to the individual bird's singing light intensity, or both. When localities as far removed from one another as our two study areas show a consistent difference, however, an examination of the comparative daybreak performance of other species seems warranted.

Difference between localities.—By using data from 1944, which are the most abundant, we see that the daybreak song of five other species occurred later in town (table 4). To make this comparison, each record at the farm was matched with a chronologically equivalent record from town. The Robin was eliminated from consideration because the single male at the farm had no rivals, sang very little, and ended his territorial song for the season on July 5; his average daybreak song was 33 minutes later than the average time for 10 territorial males in town.

Sunrise occurs one minute later in town than at the farm during the June solstice, but this could hardly account for the difference. The possibility of smog in town reducing light was rejected because the second half of the season, when little or no smoke is produced in town, shows the same tendency as the first half. The terrain is slightly more rolling in town, and there are houses casting shadows in which roosting sites occurred. However, some equally attractive sites were not so affected. Some 15 years apart the

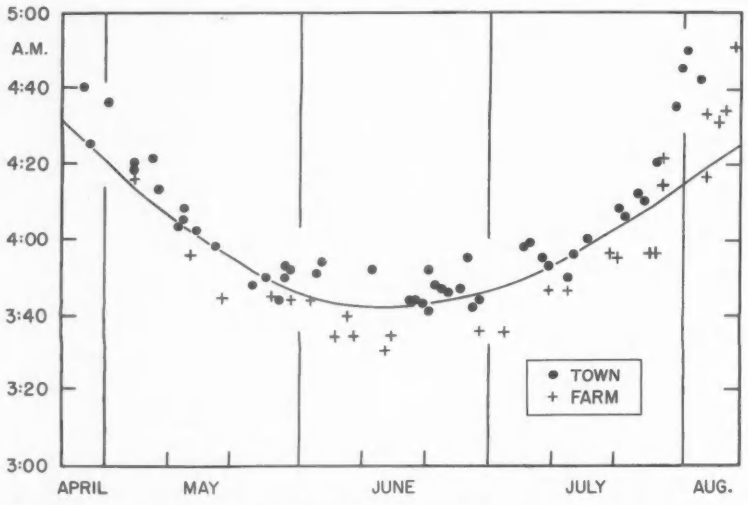

Fig. 4. Earliest daybreak song of the House Wren (*Troglodytes aedon*) at the two study areas on clear mornings only, 1944 to 1946, in relation to the beginning of civil twilight.

authors independently considered the question of why the difference should exist, and neither has been able to explain it.

Types of song curves.—There are at least three, possibly four, types of daybreak song curves in Leopold's data. First, a curve of the type represented by the Field Sparrow (fig. 1) departs from and then returns to the civil twilight curve at about the same angle on both sides of the solstice. Second, the daybreak song of the Cardinal (fig. 3) departs from the civil twilight curve at a medium angle until about the time of the solstice, after which the return to civil twilight curve is at a sharper angle. Third, the daybreak song curve of the House Wren follows the civil twilight curve so closely that it is virtually represented by it (fig. 4). A fourth possible type, obscured by much irregularity, is the song of the Catbird (fig. 2), which becomes earlier in a short time and then occurs later at a more gradual rate.

The Mourning Dove appears to be of the first type (Allard, 1930; Leopold, MS). The Song Sparrow (Nice, 1943), Rufous-sided Towhee (Davis, 1958), and perhaps the majority of song birds are of the second type. Armstrong (1955) found that the European Wren arose at about the same light intensity throughout the year so that it would appear to fall in the third category. However, we cannot find a published parallel for the Catbird.

A curve of different shape could be plotted in the Arctic where, according to Palmgren (1935) and Tinbergen (1939), birds begin to sing relatively later in relation to sunrise as the summer solstice approaches and the hours of darkness fall below the number required for sleeping.

Influence of moonlight.—Since the weak light intensity preceding the beginning of civil twilight is sufficient to stimulate daybreak song in the Field Sparrow, Catbird, and Cardinal (figs. 1, 2, 3), the question arises whether moonlight, with or without supplementary twilight, affects song curves.

TABLE 4

DIFFERENCE IN THE TIME OF DAYBREAK SONG BETWEEN THE TWO STUDY AREAS IN 1944

Species	Period	No. days	Mean time		Minutes earlier at farm
			Farm	Town	
Mourning Dove	April-June	16	4:12	4:16	4
	July-Sept.	12	4:02	4:07	5
	April-Sept.	28	4:08	4:12	4
Cardinal	April-June	8	4:08	4:13	5
	July-Aug.	9	4:02	4:13	11
	April-Aug.	17	4:05	4:13	8
Catbird	May-June	8	3:33	3:48	15
	July	7	3:42	3:48	6
	May-July	15	3:37	3:48	11
House Wren	May-June	10	3:47	3:59	12
	July-Aug.	11	4:05	4:16	11
	May-Aug.	21	3:56	4:08	12
Brown Thrasher[1]	May-June	5	3:53	4:07	14
Baltimore Oriole[2]	May-June	9	3:50	4:20	30
All species		95	3:58	4:08	10

[1] *Toxostoma rufum*; [2] *Icterus galbula*.

A zenithal full moon can produce up to 0.02 foot-candle (Humphreys, 1929), but since this condition does not occur north of Florida, the light intensity at full moon in Wisconsin is considerably less. Leopold in 1945 and Eynon in 1959 found the intensity to be less than the minimum capability of our meter, or less than 0.012 foot-candle under Wisconsin conditions.

Wright (1912) believed that moonlight was without influence, but in his second paper (1913), he reported that it had apparently affected a few of the species at his study area on the morning following a full moon in June. Haecker (1916) and Zimmer (1919) stated that the moon had no influence. Allard (1930) considered the effect of moonlight, but found his data insufficient to enable him to draw any conclusion. Nice (1943) stated that the moon is important just before and after it is full for crepuscular birds and diurnal birds that start singing very early, but she gives no data to support this conclusion for diurnal species.

Leopold suspected that moonlight affected daybreak song in the Robin on five mornings and in the Catbird and Field Sparrow each on single but separate mornings in 1944. Morning moonlight was frequently obscured by cloudiness in 1944, and Leopold tentatively felt that early singers might respond sporadically to moonlight.

When Eynon worked up the data on the Robin for 1945, however, the influence of the moon in March, April, and May was obvious (fig. 5). It is apparent that three, possibly four, daybreak songs were affected in March, four in April, and five in May. For those who might question the records as much as 2 and 3 days ahead of full moon, we point out that Leopold was often up and about more than an hour and a half before sunrise, or before the moon set.

Moonlight in June apparently was ineffective and did not arrest the more or less steady trend of the Robin to sing later and later after the solstice until daybreak song crossed the curve of the beginning of civil twilight in mid-July. This postsolstice trend is of annual occurrence in the Robin; it is apparent in all 4 years of the Leopold data and was verified by Eynon for 1959 and 1960. Armstrong (1955) found that of 119

observations on the arising of the European Wren 9 of the 13 earliest were on moonlit mornings; he concluded that it was probable that moonlight accelerates the arising time.

Moonlight also exerts an influence on species that are active in the dark. The well-known papers by Wynne-Edwards (1930) and Ashmore (1935) on the Nightjar (*Caprimulgus europaeus*) agree on the influence of moonlight on the *churring* time of this species. The first evening songs are delayed by moonlight, and singing starts earlier in

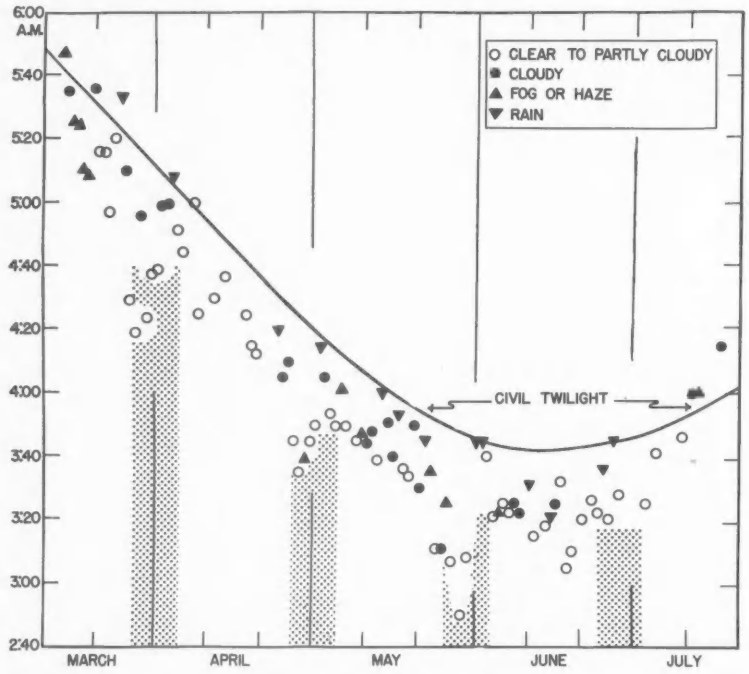

Fig. 5. First daybreak song of the Robin (*Turdus migratorius*) at the town study area in 1945 in relation to the beginning of civil twilight, weather, and moonlight. Stippling indicates periods from one day before full moon to last quarter.

the morning. Wynne-Edwards postulated a frequently quoted lunar periodicity in copulation and ovulation, but his admission that any such connection could be fortuitous (p. 244) seems to have been overlooked.

The Common Nighthawk (*Chordeiles minor*) showed a similar reaction to moonlight in the morning. Eynon recorded through the early morning hours of July 9, 1960, a clear night with full moon, and the first call of this species was heard at 2:38 a.m. with the bird "booming" shortly thereafter. In striking contrast, the bird was first heard at 3:26 on the following morning in completely overcast weather. The average time for the first call by the nighthawk on six clear mornings in July, 1959, was 3:10 a.m. Inasmuch as the Common Nighthawk starts hawking for insects in the evening and stops in the morning at higher intensities of light than the Nightjar, the only data that would be influenced by moonlight would be the first calling and the first booming in the morning.

From his manuscript and journals, it is obvious that Leopold suspected that the American Woodcock (*Philohela minor*), to be discussed later in another connection, stopped *peenting* earlier on moonlit mornings, possibly because it had *peented* and sky-danced all or most of the night. Visits to the farm coinciding with clear, moonlit nights were too infrequent to permit any firm conclusion on this point.

Role of hormones.—Allard (1930) thought it possible that the hormonal changes associated with activities of the testes were responsible for the increased sensitivity to low light intensities before the solstice, and Wynne-Edwards (1931) stated that the maturity of the gonads influenced the time at which Starlings (*Sturnus vulgaris*) awakened in the morning. Davis (1958) showed a close correlation between singing behavior and the gonad cycle in the Rufous-sided Towhee. The song season in this towhee began with the initial increase in the number of Leydig cells in the interstitial tissue, and the daybreak song became decidedly earlier when the males reached full breeding condition.

Leopold was convinced that the hormonal balance was more influential than temperature or other factors in determining song curves, but he did not have the opportunity to prove it. He was much interested in the daybreak crowing curve of the Ring-necked Pheasant, which shows the same general characteristics as the song curve of many passerines. Data have subsequently been collected by Greeley and Meyer (1953) that show the relationship between earlier crowing and stimulation of the testes in the region of our study. These investigators determined the mean gonadal weight and gonadotropin production of pheasant cocks at the game farm at Poynette, Columbia County, Wisconsin, which is just east of a line between our town and farm study areas. Their study was made between July, 1947, and June, 1948. Eynon believes that the crowing curve by Leopold and the data of Greeley and Meyer can be combined (fig. 6) because of the close proximity of Poynette, and because the periods of the two studies overlap. Leopold recorded daybreak pheasant crowing in 8 months of the year. Fall crowing began in September with the imperfect, juvenal crow which Leopold entered as "cackles" to separate such notes from the true, 2-note crowing with the accompanying wing-whir. By October, true crowing was heard, but it was not determined whether this represented the maturation of adult song in young cocks or the temporary resumption of territories by old ones. Greeley and Meyer (1953) found no increase in testis weight, but gonadotropin output by the pituitary increased from an August low until October. Testes that they examined in early October showed considerable histological advancement. Hiatt and Fisher (1947) reported that immature testes in the Ring-necked Pheasants that they studied in Montana developed in the fall and then involuted slightly.

The crowing curve of the Ring-necked Pheasant appears to be clearly correlated with gonadotropic activity of the pituitary, and presumably this is the case with passerines that sing earlier and earlier as the spring advances. However, in these species, fall song may or may not be related to hormonal activity. Blanchard (1941) and Miller (1948) reported fall singing in examples of *Zonotrichia* with inactive gonads. Marshall (1951) found that fall sexual display in male European Robins and Rooks (*Corvus frugilegus*), including frequent song in the former, occurred after regeneration of the Leydig cells in the gonads. Davis (1958) reported a limited amount of fall singing in the Rufous-sided Towhee as well as a slight increase in the number of Leydig cells in a few juvenal birds.

LIGHT INTENSITIES

Light intensities for civil twilight.—The beginning of civil twilight on clear mornings is a reliable and useful measure of equal light intensity because it is the time when the center of the sun is 6° below the horizon regardless of its declination on the par-

ticular day. Humphreys (1929) listed a value of 0.4 foot-candle for this position of the sun, but Nice (1943) found that 21 readings in Ohio averaged 0.217 foot-candle; her meter was not adapted to measure low intensities.

Of the hundreds of readings recorded by Leopold for daybreak song on clear mornings, there are 21 which happened to coincide with the minute at which civil twilight began, and these have a mean value of 0.029 foot-candle which matches the only read-

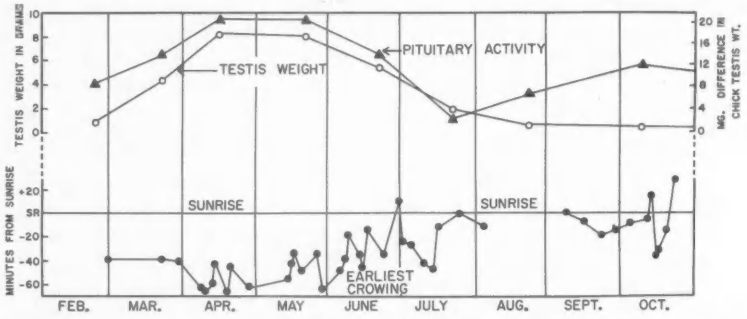

Fig. 6. Earliest daybreak crowning by the Ring-necked Pheasant (*Phasianus colchicus*) on clear mornings, 1944 to 1947, in relation to sunrise and to the annual cycle of testis and pituitary activity as determined by Greeley and Meyer (1953) for Poynette, Wisconsin.

ing (0.03) taken very soon after the instrument had been recalibrated. From its beginning until after the start of civil twilight, the light intensity at dawn increases in an exponential manner with respect to time. When one selects a clear morning with a sufficiently large and varied number of species in song, a curve of the increase in light can be drawn by plotting light intensities of daybreak songs on the ordinate against their time on the abscissa. The point at which such a curve is intercepted by a vertical line from the abscissa at the minute of the beginning of civil twilight yields a close approximation of the light intensity at that time. Eynon plotted five such clear dawns from Leopold's data at the height of the song season in May and June. A range of from 0.033 to 0.07 with a mean of 0.046 foot-candle resulted. After the foot-candle meter used in this study had been thoroughly checked and recalibrated in the fall of 1959, Eynon found that on 4 clear days at the start of civil twilight in the morning and 4 clear days at the end of civil twilight in the evening, the light ranged from 0.03 to 0.05 with a mean of 0.039 foot-candle at Madison, Wisconsin.

Scheer (1952) cites values recorded at sea by Rosenhagen (1949) that show civil twilight starting at 2 luces (0.186 foot-candle). It would seem reasonable to expect measurements taken in terrestrial habitats to be somewhat lower than those from the open sea where illumination would be maximum. Leopold's data suggest the possibility that previously reported light intensities for the beginning of civil twilight in terrestrial habitats may be too high. Because daybreak singing begins within a few minutes of this position of the sun, the verification or refutation of this premise appears worthy of the attention of those workers who have suitable instruments available.

Light intensities at time of daybreak song.—The light intensity at which many birds begin their daybreak song is so low that most investigators have been hampered by the necessity of trying to estimate the readings on their photometers if daybreak song came at an intensity of less than one foot-candle. In a large measure, Leopold overcame this

TABLE 5

LIGHT-INTENSITY VALUES IN FOOT-CANDLES FOR FIRST DAYBREAK SONG, 1945 TO 1948

Species	March N	March Mean ±2 S.E.	April N	April Mean ±2 S.E.	May N	May Mean ±2 S.E.	June N	June Mean ±2 S.E.	July N	July Mean ±2 S.E.
Ring-necked	6	.014	8	.013±.002	5	.031	4	.105	3	.417
Pheasant[1]	3	.021	4	.024	1	.030			3	.150
Mourning	8	.028±.012	16	.045±.028	18	.023±.006	18	.037±.014	12	.040±.022
Dove	2	.026	11	.051±.040	7	.029	4	.040	3	.150
Great Crested					6	.061	4	.166	3	.165
Flycatcher[2]									1	.100
Eastern Wood					2	.014	2	.018	6	.014
Pewee									2	.019
House Wren					19	.039±.018	19	.055±.012	12	.053±.032
					8	.053±.022	4	.067	5	.037
Catbird					9	.013±.002	15	.018±.004	5	.060
					3	.026	4	.019	4	.035
Brown			1	.050	8	.022±.008	3	.095		
Thrasher			2	.046	2	.070			1	.020
Robin	15	.013±.001	24	.023±.008	19	.015±.002	17	.016±.004	8	.043±.044
	6	.041	12	.017±.004	7	.014	6	.016	3	.044
Eastern	1	.050	10	.029±.016	8	.019±.004	5	.016	6	.047
Bluebird[3]	3	.024	4	.029	1	.020			3	.125
Warbling					3	2.400	2	.375	4	4.300
Vireo[4]									2	.325
Yellowthroat					5	.012	1	.012	10	.020±.006
									3	.018
Eastern	1	.080	5	.110	4	.056	1	.050	1	.050
Meadowlark[5]	2	.200	2	.020	1	.020			1	.300
Redwinged	3	.043	7	.041	3	.800			1	5.000
Blackbird	2	.250	2	.050					1	.050
Baltimore					7	.191	7	.161	1	6.000
Oriole					1	.040	1	.150	2	.350
Cardinal*	29	.032±.012	20	.022±.006	12	.033±.030	15	.034±.006	9	.036±.018
	20	.085±.072	7	.067	6	.352	3	.107	4	.026
Indigo					4	.014	4	.022	9	.074±.106
Bunting[6]									2	.015
Rufous-sided			1	.020	7	.014	4	.022	7	1.437
Towhee			1	.040	1	.030			2	.014
Chipping					7	.027	3	.019	2	.160
Sparrow[7]					1	.050				
Field	1	.040	13	.022±.005	9	.012†	4	.015	10	.013±.002
Sparrow	1	.050	4	.022	1	.020			4	.012
Song Sparrow	2	.025	11	.015±.005	8	.014±.002	4	.014	7	.060
	5	.052	6	.023					2	.033

[1] Values on the upper line are for clear to partly cloudy skies, and those on the lower are for cloudy to overcast. Standard error of the mean computed only when readings per month total 8 or more.

[2] *Myiarchus crinitus*; [3] *Sialia sialis*; [4] *Vireo gilvus*; [5] *Sturnella magna*; [6] *Passerina cyanea*; [7] *Spizella passerina*.

*Readings for the Cardinal before March are 0.018 ft.–c. for the clear dawn of January 7, 1948, and six readings for clear February dawns with a mean of 0.036 ft.–c.

†All values 0.012 for May.

difficulty through the use of the General Electric foot-candle meter described in the first part of this paper. However, it turned out that some daybreak songs were given at values lower than the minimum capability of the instrument. After a few attempts to estimate a fraction of 0.012, Leopold abandoned this for the notation "–0.012," which occurs in his notes occasionally for the Ring-necked Pheasant, Mourning Dove, Catbird, Yellow-throat (*Geothlypis trichas*), Cardinal, Field Sparrow, and Song Sparrow at the farm, and frequently for the Robin in town. In order to handle the statistics, Eynon read all values so indicated as 0.012.

In table 5 the species have been arranged in phylogenetic order. To put them in order of increasing light intensity would require a separate table for each month. These data are for both study areas combined, but records for the Robin at the farm are excluded for reasons given earlier in this paper. The light intensities in this table are the lowest ever reported for daybreak song in North American birds. It therefore becomes necessary to consider their relative accuracy. Recently, values in the same range have been reported for European species by Scheer (1952) and Groebbels (1956). Readings comparable to Leopold's "–0.012" converted to foot-candles from the luces reported by these authors are 0.003 for the European Wren, 0.004 for the Great Reed Warbler (*Acrocephalus arundinaceus*), 0.007 for the European Blackbird and the Redstart (*Phoenicurus phoenicurus*), and 0.008 for the Reed Bunting (*Emberiza schoeniclus*). Peterle (1955) found that the first call of the Red Grouse (*Lagopus scoticus*) averaged 0.39 lux (0.036 foot-candle) for 10 mornings, but on four occasions it came at a light intensity of 0.1 lux (0.009 foot-candle). Thus our figures seem reasonable and may be presented with a fair degree of confidence.

Table 5 is self-explanatory, but at first glance the data suggest that some species appear to require more light for daybreak song on cloudy mornings early in the year. This may be seen in the values for Ring-necked Pheasants, House Wren, Catbird, Red-winged Blackbird (*Agelaius phoeniceus*), Cardinal, Rufous-sided Towhee, and Song Sparrow. The light intensity shifts to lower values for cloudy mornings as opposed to clear for these species in July. This is suggestive of a possible temperature relationship, since cloudy days in spring generally coincide with lower temperatures which might delay song, but lower temperatures in July are probably stimulating in the midst of heat, which Nice (1943) considered as having an inhibiting effect. However, in those species where the monthly data by Leopold are adequate for statistical testing, the difference in the light intensities between clear or partly cloudy mornings and cloudy or overcast mornings is not significant.

According to Scheer (1952), it was Haecker (1916) who first clearly stated that light intensity, modified by cloudiness, determined the time of daybreak song. Numerous authors have subsequently agreed on this point: Song is delayed on cloudy mornings until the illumination reaches the approximate intensity at which it would have started had the morning been clear. To demonstrate the delay, we have selected the two species that are the earliest singers at town and farm, respectively, the Robin and the Field Sparrow (table 6).

Light intensities at evening song.—Numerous investigators have found that daily cessation of bird song comes at light intensities higher than those at which it begins in the morning. Wright (1912, 1913) in America and Haecker (1924) in Europe were fully aware that the interval between sunset and the last song of the day was considerably shorter than that between daybreak song and sunrise. Allard (1937) commented upon the inconsistency of song and other activities near the close of the day as compared to dawn. Nice (1943) determined the ratio of the light intensity of evening song to that

of daybreak song in the Song Sparrow. More recently Grimm (1957) confirmed the earlier work by Heyder (1933) on the evening song of the European Blackbird by taking readings on 146 evenings. He then compared his mean values to the morning values reported by Scheer (1952) and found that the light intensity at the end of the evening song period was 10 to 30 times as high as that of daybreak song, depending on the phase of the annual cycle.

TABLE 6

DELAY OF DAYBREAK SONG ON CLOUDY MORNINGS, 1944 TO 1947

		April		May		June		July	
		No. days	Minutes before sunrise	No. days	Minutes before sunrise	No. days	Minutes before sunrise	No. days	Minutes before sunrise
Robin	Clear[1]	26	48	18	66	18	62	15	48
	Cloudy[2]	12	41	13	50	11	52	3	27
	Mean delay		7		16		10		21
Field Sparrow	Clear	13	36	9	52	6	64	14	58
	Cloudy	6	32	2	41	1	47	4	55
	Mean delay		4		11		17		3

[1] Includes partly cloudy.
[2] Includes complete overcast, but excludes days with rain, fog, or haze.

Leopold's data for evening light intensity are not as abundant as those for morning, and since the values are so much higher, they are not carried beyond two decimal places (table 7). The variance is high and inconsistencies are apparent. In some cases, the range of values from which the means were computed for clear or partly cloudy evenings is greater than that for cloudy or overcast evenings. This is due in part to fewer readings on evenings of the latter type. More important, however, is the tendency for evening song not to have the precise relationship to light as does daybreak song. With a few exceptions, the mean values for cloudy or overcast evenings are higher than for clear, the disparity being much greater than for daybreak song. The birds not only stop singing earlier on cloudy evenings in respect to sunset or the end of civil twilight, but they appear to do so at a higher absolute light intensity. This cloudiness effect on evening song has also been found in detailed studies of single species (Nice, 1943; Armstrong, 1955; Grimm, 1957).

The characteristic light intensity that governs daybreak song does not have a parallel in the evening cessation. Rather there seems to be a range of intensities in which the last song may occur, and the lower limit of such a range is generally higher than the light intensity for daybreak song. The recording of the last song of any diurnal species on our study areas never required a light, whereas it was impossible to read a watch at the intensities at which the earliest daybreak songs occurred for much of the season. There are exceptions to the general rule that diurnal birds stop singing in more light than that at which they begin. McCabe (1951) found that the Traill Flycatcher (*Empidonax traillii*) regularly sang until it was completely dark during its unique evening song period. Eynon (1951) found that the evening flight song of the Ovenbird (*Seiurus aurocapillus*) was given at light intensities too low to read a watch without the aid of a flashlight. Indeed, the exceptions may be confined to species with special flight songs or those which sing on the wing much of the time. Eynon has heard the Eastern Kingbird

TABLE 7

MEAN LIGHT INTENSITIES IN FOOT-CANDLES FOR EVENING SONG, 1945 TO 1947

Species	April N	April Mean	May N	May Mean	June N	June Mean	July N	July Mean
Ring-necked Pheasant[1]	7	2.13	6	3.26	0		0	
	0		0		0		0	
Mourning Dove	7	2.34	8	0.85	3	3.53	6	3.87
	0		0		2	10.15	3	5.00
Great Crested Flycatcher			6	0.12	2	0.12	5	6.28
			0		2	0.78	3	4.73
Eastern Wood Pewee			4	1.13	3	0.09	6	0.07
			0		3	0.23	2	0.55
House Wren			7	0.26	4	0.93	6	2.95
			0		2	4.80	3	3.33
Catbird			7	0.03	5	1.73	3	0.33
			0		4	0.24	3	0.55
Robin	6	0.54	5	2.86	6	0.50	0	
	0		0		0		0	
Yellowthroat			7	0.08	2	2.70	6	6.17
			0		3	0.14	0	
Eastern Meadowlark	7	0.85	7	5.38	3	3.93	0	
	0		0		0		0	
Redwinged Blackbird	5	4.92	6	0.75	0		2	13.25
	0		0		0		3	7.67
Baltimore Oriole			6	5.67	3	4.25	0	
			0		0		0	
Cardinal	6	0.59	3	1.00	2	0.50	6	1.19
	0		0		0		3	4.17
Indigo Bunting			4	0.51	2	1.00	6	8.92
			0		0		0	
Rufous-sided Towhee			3	2.47	3	0.60	5	6.74
			0		2	4.58	3	8.00
Chipping Sparrow			6	0.15	2	10.05	0	
			0		2	0.13	0	
Field Sparrow	6	0.24	9	0.21	4	1.34	7	2.07
	0		0		4	2.31	3	0.57
Song Sparrow	10	0.62	8	3.76	4	1.75	2	6.50
	0		0		3	5.17	0	

[1] Values on upper line are for clear to partly cloudy sky, and those on lower are for cloudy to overcast.

(*Tyrannus tyrannus*), Horned Lark (*Eremophila alpestris*), and Yellowthroat performing in the evening twilight when it was much too dark to see the birds.

COMPARISON OF DAYBREAK AND EVENING SONG

Diurnal species.—The ratio between light thresholds at daybreak and evening has been reported for only a few species in terms of actual incident light values. In the purest sense, each species should be compared for relatively short periods of the annual cycle (tables 5, 7). The Robin in July is not the same bird it was in April. If clear daybreaks are compared to clear evenings for each month, weather factors should average out over a 3- to 4-year period. However, it is probable that each species changes its hormonal balance and reproductive status at a different rate each year and that between species rates are rarely comparable. With these facts in mind, we present the composite data on light intensity at daybreak song and evening song (table 8). We have restricted this table to species for which the data by Leopold contain at least 15 evening readings for the 3 or 4 months involved. Once again the figures are influenced by more morning readings in five species, and the ratio is affected by the tendency of many species to stop

singing proportionately earlier in relation to evening civil twilight after the solstice. Evening song fails before daybreak song.

The species in table 8 have been arranged in ascending order of daybreak light values, but the evening intensities show no corresponding order. This is a reflection both of the lack of precision in the relationship of evening song to light and of a seasonal waning of the impulse to sing.

TABLE 8

RATIO OF FOOT-CANDLES AT DAYBREAK SONG TO EVENING SONG, 1945 TO 1947

Species	(a) Daybreak No. days	(a) Daybreak Mean value	(b) Evening No. days	(b) Evening Mean value	(c) Ratio (a):(b)
Field Sparrow	36	0.016	26	0.96	1:60
Robin[1]	68	0.021	17	1.20	1:57
Catbird	29	0.024	15	0.66	1:27
Song Sparrow	30	0.025	24	2.35	1:94
Cardinal	56	0.030	17	0.86	1:29
Mourning Dove	64	0.036	24	2.36	1:66
Yellowthroat	16	0.040	15	2.86	1:72
House Wren	50	0.048	17	1.37	1:29
Eastern Meadowlark	11	0.080	17	3.26	1:41

[1] Omits farm; no evening readings in July for town.

The fact that most diurnal birds stop evening song when there is more light than that for daybreak song raises the question of why this should be so. Provided the same day is calm and clear at both daybreak and evening, there are usually no other environmental changes except temperature and sometimes humidity, and the light increases and wanes at the same rate. Temperature correlation attempts have not been very successful (Shaver and Walker, 1931; Elliott, 1932). It appears that there is a factor operating at evening, either in the bird or in the environment, which is not present, or is different, at daybreak.

Crepuscular species.—The singing behavior of crepuscular species, which begin activity in the evening after a day's rest, should yield some insight into this question. To this end, Leopold used the American Woodcock as a test case. Several males performed annually at the farm, and a special effort was made to record this species. The times and light intensities of the first and last *peent* at evening and morning were used, respectively, as equivalents of the daybreak song and evening song of diurnal species. Some defense of this hypothesis seems justified.

We agree with Pitelka (1943) that *peenting* serves as a warning and advertisement for this species. While *peenting* usually precedes the first song flight of the evening and continues between flights, Leopold's records show that the song flight can occur without *peenting*. From this it would appear that *peenting* is equivalent to the territorial song in passerines. The *peent* note is rare after the end of the spring sky-dancing period in early June, but Leopold recorded it twice in 1944, once on July 4 and again on October 17.

At the farm the first *peent* of the evening usually came well before the end of civil twilight, occurring later on only three evenings out of 61 (fig. 7). The last *peent* at daybreak, however, occurred before civil twilight began on 22 mornings out of 45 (fig. 8). A tendency to delay *peenting* on clear evenings and to begin earlier on cloudy ones is evident, as is a trend toward earlier cessation on clear mornings. It seems apparent that the American Woodcock, at evening, is stimulated by a certain intensity of darkness and that at daybreak it is inhibited by a certain intensity of light. If light alone governed

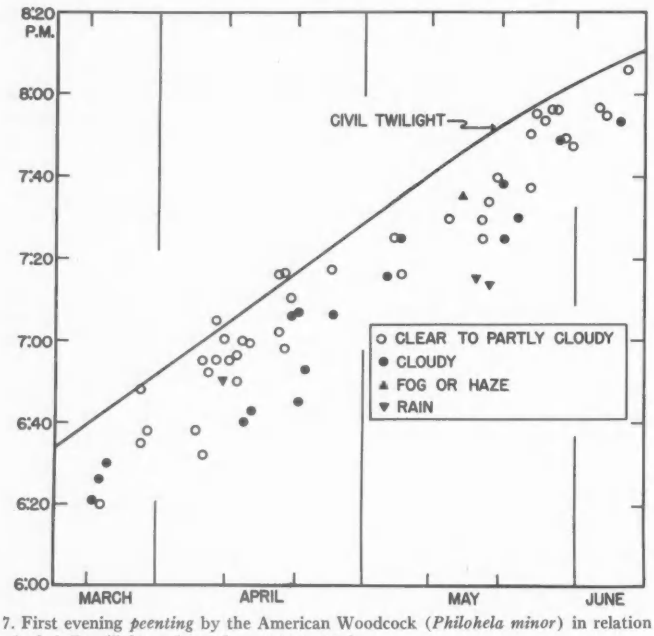

Fig. 7. First evening *peenting* by the American Woodcock (*Philohela minor*) in relation to the end of civil twilight and weather, 1944 to 1947.

the performance, the two sets of data points would yield a curve of best fit equidistant from the civil twilight curve. It takes less light to stop *peenting* at daybreak and more to start this activity in the evening.

Examination of the light measurements for clear and partly cloudy days confirm this disparity. Light-intensity values for the first evening *peent*, 1945 to 1947, ranged from 5.0 foot-candles down to 0.02 foot-candle for 24 readings. The evening mean intensity with standard error was 0.71 ± 0.26 foot-candle, but this was influenced by five high readings of 2, 2, 2.5, 3, and 5 foot-candles; the other 19 readings were not over 0.5 foot-candle. For the last *peent* at daybreak, there was an intensity range of from 0.012 to 0.06 foot-candle for 15 readings. The morning mean intensity of 0.028 ± 0.002 revealed just how precise cessation is in this species.

This disparity shows that our dark-active species, the American Woodcock, follows the same principle as that governing diurnal birds: Lesser intensities, of darkness in the former, and of brightness in the latter, stimulate song at the beginning of their respective active periods. Both kinds of birds seem to stop singing with larger quanta of light or darkness still present, in accordance with their habits, diurnal or crepuscular. The responsible factor, whatever it is, appears to be intrinsic and not due to the conditions of the environment at the time of day. In field studies of wild birds, this internal factor cannot, of course, be determined.

GENERAL REMARKS

In view of this response to light and the long-term modifying effect of hormones, two concepts should be examined. One is old yet recurrent in the literature on bird song;

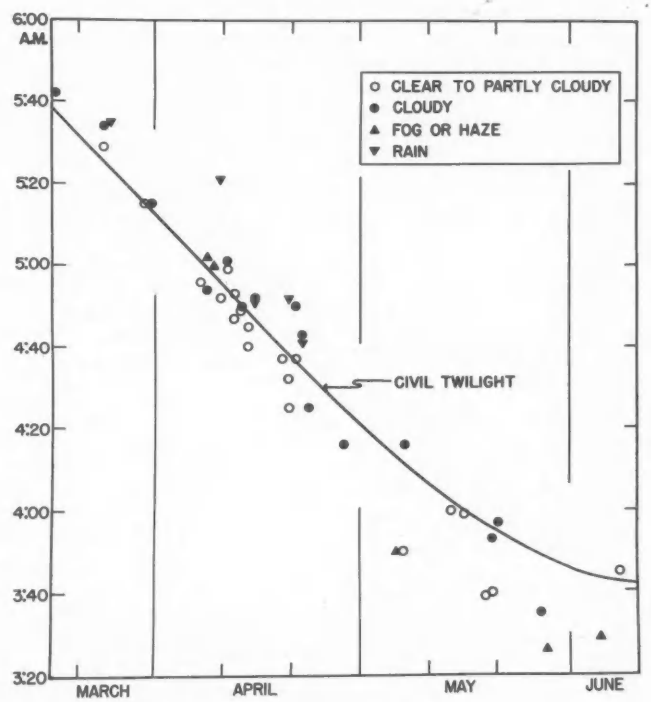

Fig. 8. Last *peenting* at daybreak by the American Woodcock in relation to the beginning of civil twilight and weather, 1944 to 1947.

the other is comparatively recent and embraces a wide variety of animals other than birds. These concepts, between them, probably account for the short-term factors regulating daybreak and evening song.

Activity rhythms.—The investigations of Kramer (1952), Matthews (1955), Sauer (1957), and other ornithologists working in the field of avian celestial navigation have demonstrated that birds have a precise sense of time. Rawson's (1954) demonstration of endogenous activity in the Starling suggests that this ability derives principally from a physiological "clock" which is reset continually by environmental clues. Aschoff (1958) called such clues "time-givers." Birds are not unique in having such "clocks," as their existence, but not their location, has been described for many classes of animals.

The study of biological periodicities, especially those of approximately 24-hour duration, has occupied the attention of a growing number of zoologists and botanists in the years since Leopold's field studies were made. Rhythms with a period of about one day, until recently called diurnal or daily, have now been designated as "circadian." Harker (1958) and Aschoff (*op. cit.*) have reviewed the literature on circadian rhythms in animals.

Among the more easily recorded circadian rhythms in birds are the times at which communal and hole-roosting species leave their roosts or return to them, the time of

arrival of lek species at their dancing grounds, and the time of daybreak and evening song. Of these, daybreak song offers the best opportunity to the investigator who wishes to study a number of species simultaneously.

Purely endogenous or free-running circadian rhythms can be determined with certainty only by isolating animals in a controlled environment. In most animals, 24-hour periodicities modified by daily environmental clues are entrained circadian rhythms with both exogenous and endogenous components.

The daybreak activity pattern of spontaneous awakening some time before daybreak song suggests such a combination in birds. Scheer (1951) reported a quiescent period for the European Robin, European Blackbird, and Chaffinch between the time they awoke and their subsequent daybreak song, and he thus confirmed Allard's (1930) premise that birds are "awaiting alert for the coming of the dawn." Presumably such spontaneous awakening is caused by an endogenous factor. Here it becomes necessary to introduce the concept of anticipation: the bird awakens in darkness without benefit of environmental clues. Once awake, the bird can sample the light, and daybreak song occurs when the proper intensity is reached.

This hypothesis of an anticipatory period during which the bird samples or tests the light intensity is supported by the behavior of other animals. Hodgson (1955) found that worker leaf-cutting ants (*Atta cephalotes*) appeared at the nest entrance about an hour before dawn but never left to forage until the light intensity on the forest floor reached 0.3 foot-candle. Departure time was advanced or delayed according to whether the investigator supplemented the normal light intensity with a lantern or retarded it with an awning. Twente (1955) reported that cavern-dwelling bats, principally *Myotis velifer*, appeared near the entrance in increasing numbers as the light diminished, and that the general emergence was preceded by short sorties by a few bats, out and back. The length of these sorties increased from a few feet up to 50 yards over a 15-minute period.

The only evidence against spontaneous, endogenous awakening is to be found in the influence of moonlight. The Nightjar and Common Nighthawk could easily have been awake most of the night, but the Robins, which in 1945 began to sing from 20 to 40 minutes earlier on moonlight mornings in May (fig. 5), presumably had been asleep. A possible explanation is that the Robin awakens normally at this season as much as 20 to 40 minutes before singing, and that it responds differently to the "clock" when there is more light.

Under controlled conditions, one of the criteria used by most workers in a test for a physiological "clock" is that the beginning of the active period should drift if no environmental synchronizers are available to the animal. The most potent of these synchronizers is light. De Coursey (1961) demonstrated control of the activity phase of 24-hour rhythm in the flying squirrel (*Glaucomys volans*) in an intensive study of both wild and laboratory animals. She found that light reset the "clock" by interacting with the endogenous rhythm but could not demonstrate such entrainment to either sound or temperature stimuli.

The comparative lack of precision in the evening song of most diurnal birds may indicate a reduced dependence on the endogenous rhythm at the close of the active period. Armstrong (1954) suggested that decreased light may have provided the principal cue for reducing activity in Arctic birds. It would appear that in the temperate zone, where the decrease of light is much faster, such a cue would be even more effective. Palmgren (1935) pointed out that most passerines in northern Lapland rested in the evening and resumed activity as much as 4 hours before midnight and that temperature

and humidity controlled the period of activity. He also stated (Palmgren, 1941) that the "autonomy of the internal rhythm" was involved at both awakening and roosting. An endogenous factor at cessation of song is difficult to document. The rather abrupt cessation of song by the Traill Flycatcher in darkness, reported by McCabe (1951), could be due to such a factor.

Fatigue theory.—Wright (1912) stated that fatigue caused the diurnal birds on his study area to stop singing in the evening with more light than that at which they had started in the morning. His idea was echoed by Haecker (1924), Allard (1930), and Nice (1943). Armstrong (1954) put the same hypothesis in more modern terms when he concluded that "apparently waning of the drives stimulating diurnal activity leaves the field open for the factors inducing sleep." The foregoing statement applied to birds in the continuous light of the Arctic, but Armstrong (1955) implied that, in the lower latitudes with a definite night, hunger was one of these drives. The European Wren, he found, varied its roosting time less in midwinter than in midsummer, and he suggests that in the former period, the bird does not roost until the light is so dim that foraging is "unprofitable." In summer, however, Armstrong suggests that this wren roosts at a higher light intensity because there is adequate food and "there is no pressure to stay up."

Craig (1926, 1943) attempted to demolish the fatigue theory. He raised the valid objection that in the evening not only the end, but also the beginning, of the song period in diurnal birds occurs at higher light intensities than those which govern the morning performance. He claimed, quite justly, that this earlier beginning is hardly consistent with fatigue. Since Leopold did not study the beginning of evening song nor the end of morning song in any diurnal species, we cannot debate the issue. Craig also suggested anticipation which, with regard to evening song, seems to have no more validity than fatigue. Armstrong (1955) also found Craig's use of the term inadequate. McCabe (1951) suggested that the beginning of the evening song of the Traill Flycatcher was probably controlled by light intensity, but that its cessation in the dark quite certainly was not. While not eliminating the possibility of fatigue, the last worker suggested a fading external stimulus, "irrespective of whether the bird is physically able to respond or not," as an alternative hypothesis. McCabe's suggestion appears to have much merit for species in which light is not a factor. The failure to respond may be due to the "monotony-threshold" of Hartshorne (1956). The song of the Traill Flycatcher would seem to come under Hartshorne's definition of the nonversatile, discontinuous singer.

Leopold, to the best of our knowledge, was the first to test the fatigue theory on a crepuscular or nocturnal bird. The papers on the Nightjar by Ashmore (1935) and Wynne-Edwards (1930), referred to earlier, reported only on the beginning of song during both twilight periods of the day. However, Hansen's (1952) data on the Tawny Owl (*Strix aluco*) showed that this species begins calling at a time closer to sunset than morning cessation comes in relation to sunrise. Leopold suggested the Whip-poor-will (*Caprimulgus vociferus*) as another test species, but birds of this species were generally too distant at the farm to provide reliable data. The caprimulgids vary so much among the different species that they may not be a happy choice. Brauner (1952), for instance, reported that the Poor-will (*Phalaenoptilus nuttallii*) both begins and ceases activity at about the same light intensity of less than one foot-candle. Except during migration, the Common Nighthawk is normally active around dusk and dawn, with a silent period during the middle of the night. Eynon heard this species begin to call on July 26, 1960, at 2:05 a.m., or over an hour ahead of the average time of its first call at this season. There had been a series of violent thunderstorms lasting throughout the normal active period on the previous evening. Eynon's premise is that the birds were unable to forage in the evening and that the earlier than usual foraging in the morning was due to a hunger drive.

Leopold's use of the American Woodcock as a test of the fatigue hypothesis does not prove its validity, however. We have shown that diurnal species begin to sing at daybreak at a rather precise light intensity, but the evening song intensity has a greater variance. By this criterion, the American Woodcock is the exact opposite, for it is the last song at daybreak that is precise. Allard (1937) studied the evening departure and the morning arrival of a pair of Screech Owls (*Otus asio*) at their roost in relation to sunset and sunrise. Using time rather than intensity, he also found a higher correlation in the morning. This led him to discard the fatigue theory to which he subscribed in his earlier (1930) paper and to account for the greater variation found in the evening in both diurnal and nocturnal birds as possibly "dependent upon differences in the sensitivity and adjustment of eyes that have become light-adapted and those that have not."

Grimm (1957) quantified pauses in the songs and calls of the European Blackbird for 37 evenings as a measure of disturbance susceptibility or fatigue. He combined the results of all evenings to suppress daily randomness and obtained an exponential curve showing the progressive pauses in evening vocalization up to cessation. However, this curve could measure a fading external stimulus or the waning of drives as readily as it measures fatigue. If there is any merit in the fatigue theory, Grimm's approach seems to be the most promising technique for use in the field, but laboratory studies are necessary to prove that the activities of an average day are sufficient to produce true fatigue in a song bird on its breeding territory.

Ehrström (1956) summarized reports by 107 observers during the solar eclipse of June 30, 1954. Totality occurred in the early afternoon, and the songbirds stopped singing for about 15 minutes. In general, they started to sing after the eclipse at a much higher light intensity than that at which they had stopped beforehand. This reversal of the usual relationship of song to waning or increasing light could be used to justify the fatigue theory of evening cessation of bird song as well as to demonstrate the rhythmic nature of daybreak song.

Absolute light intensity as a stimulus.—There appears to be an absolute light intensity, narrow in range and subject to individual variation within each species, which provides the stimulus for daybreak song. Seasonal shifts in the mean value of this light intensity seem to be due to the reproductive status and a changing hormonal balance. But when we measure the absolute light intensity are we necessarily determining the standard that acts as the minimum stimulus for the bird? Some birds may have a higher degree of retinal adaptation than others to increasing versus decreasing light. In the final analysis, it may be the relative brightness of various components of the habitat that is appraised by the newly awakened bird. The nucleus of this intriguing idea derives from a suggestion by J. P. Ditchman (personal communication). Further discussion of relative brightness is beyond the scope of this paper, but its evaluation by the use of modern photographic techniques is conceivably the next step in the study of stimuli for bird song at low light intensities.

SUMMARY AND CONCLUSIONS

The times and light intensities for the first daybreak or last evening songs of 20 species of birds were recorded over a four-year period at two study areas, town and farm, in southern Wisconsin. A daily record of daybreak song for five common species showed that simultaneous, interspecific failure to sing was rare. Failure to sing not due to weather ranged from zero in the Catbird to 22 per cent in the Cardinal, but an isolated Robin sang little and late. In 1944, daybreak song in six species averaged 10 minutes earlier at the farm than in town.

Daybreak song curves for the House Wren, Catbird, Cardinal, and Field Sparrow differed in their relation to civil twilight and in the tendency of each species to depart from its average time. The Robin sang much earlier on moonlit mornings in March, April, and May, 1945, but the June moon had no effect. Occasionally, the moon affected song in other species.

Close correlation existed between the earlier crowing of the Ring-necked Pheasant relative to sunrise and a curve of gonadotropic activity of pheasant pituitaries in spring; and daybreak crowing in the fall seems to be correlated with a more limited production of gonadotropin. It is suggested that a similar cycle is responsible for earlier song by passerines.

Tabulation of the light intensities disclosed that daybreak song came at lower, more precise values than evening song. The lower range came close to minimum values reported for European species. Song was delayed on cloudy mornings until light reached an intensity not significantly different from that of clear mornings. Mean light intensities at evening song ranged from 29 to 94 times higher than for daybreak song. The American Woodcocks stopped *peenting* at daybreak with more darkness than was necessary to start them in the evening, but it was cessation of song that was precise and not the beginning of song.

It seems probable that some birds, at least, awaken endogenously, test their environment during an anticipatory period, and sing when the light reaches a certain intensity. Such entrained circadian rhythms have been suggested for other animals. Cessation at evening may be due to fatigue, waning drives, or a fading stimulus, but none of these concepts nor the endogenous components in activity rhythms can be verified in the field.

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PLUMAGE DEVELOPMENT AND MOLTS OF CALIFORNIA QUAIL

By Ralph J. Raitt, Jr.

In recent years much attention has been focused on the timing of plumage development in young galliforms. The Bobwhite (*Colinus virginianus*) has been the subject of several recent studies on molts; particularly valuable are those of Petrides and Nestler (1943 and 1952) and Thompson and Kabat (1950). These studies, and others on the Bobwhite, the Scaled Quail, *Callipepla squamata* (Wallmo, 1956), the Ring-necked Pheasant, *Phasianus colchicus* (Buss, 1946; Thompson and Taber, 1948; Westerskov, 1957), and the Hungarian Partridge, *Perdix perdix* (McCabe and Hawkins, 1946; Thompson and Taber, *op. cit.*), were conducted with the aim of establishing criteria for accurate age determination based upon the stage of plumage development of young birds. Similar detailed studies had not been published for the California Quail (*Lophortyx californicus*) at the time of this study. However, following the completion of the present investigation, Williams (1959) described in detail the growth of first winter primaries of California Quail of known age in New Zealand. The present report partly duplicates that of Williams, but differences in the results obtained necessitate the presentation and analysis of data obtained in my study.

Genelly (1955:280–281) constructed graphs of replacement rates of primary flight feathers in young California Quail based on repeated captures of wild young birds and on captive young of known ages. The resulting curves agree closely with a similar curve based on the data of Petrides and Nestler (*op. cit.*) on age determination of young Bobwhites. The curves given by Genelly are adequate for the aging of most young in the field. However, in view of the paucity of information on plumage development of young of this species, it was felt that a more detailed study of the wing molts and body plumage would be desirable. Accordingly, several groups of young of known age were purchased from a dealer in Berkeley, California, in the summer of 1957, raised in cages, and their plumage development followed. Preserved specimens and dried wings of young of known age and museum study skins of wild young quail provided supplemental data.

The postnuptial molt of the adult birds is of interest as an important part of the annual cycle. Data as to the timing of this molt were obtained by the examination of live birds trapped in the course of a population study.

I wish to express my gratitude to Dr. A. Starker Leopold for advice and encouragement during this investigation, to the Museum of Vertebrate Zoology, Berkeley, California, for financial assistance, to Drs. Lewis W. Taylor and John Davis for reading the manuscript, and to Dr. Victor Lewin, Richard C. Banks, and my wife, Imogene, for assistance in various aspects of the study. Grateful acknowledgment is extended to Gene M. Christman for the execution of the figures.

METHODS

A total of 23 young quail were purchased in four lots. All but five were about one week old when they were obtained. The other five were taken directly from the incubator as they hatched. All birds in the latter group died before they were ten days old. Because of escape or death only eleven birds were raised to the age of completion or near completion of the postjuvenal molt. Although the birds from which most of the data were derived were not obtained until they were a week old, the dealer kept records on the hatching dates of the various groups and there is not likely to have been an error in the ages as given by him. The young birds were kept in a large cardboard carton with a red light bulb for warmth until they were about a month old, when they were transferred to wire cages. From one to four birds were kept in a cage. They were fed a start-

ing mash mixed with cracked corn, spread in a layer on the bottom of the cage; water was amply provided.

During the first few weeks the birds were checked daily. Subsequently, they were checked less often as plumage changes became slower. In the last month of plumage development they were examined only once every four or five days. On each examination the lengths of selected growing remiges and rectrices were measured, and changes in the several other tracts were recorded.

All wild quail trapped during the late summer and autumn were checked for signs of molt and the length and number of each growing flight feather was recorded. A total of 161 captures during four molting seasons provided the data on the postnuptial molt.

NATAL DOWN

The young quail is hatched with a full covering of down. This downy plumage gives the young bird its characteristic concealing coloration of longitudinal, dark brown stripes on a background of buff. Replacement of the natal plumage begins early, for at hatching the tiny wings show slender, short pinfeathers of the first seven primaries of the juvenal plumage. The natal down behind the eye persists until the bird is about seven weeks old.

JUVENAL PLUMAGE

The juvenal plumage begins to emerge before hatching and is not fully developed until the age of about ten weeks. Figure 1 summarizes the development of juvenal and first winter remiges and rectrices. The period of growth of the primaries spans the entire period of development of the juvenal plumage. This tract is regular in its development and shows little individual variation. For these reasons and because primaries are easy to identify individually and to measure, their development has been emphasized in establishing criteria for age determination in the California Quail, as has been the case in developmental studies of other young galliforms.

In the discussion of remiges in this paper the innermost primary is designated number 1 and the outermost number 10. The outermost secondary is number 1 and the innermost is number 15.

The young bird is hatched with juvenal primaries 1 through 7 just erupting through the skin. Of these feathers, numbers 1, 4, and 7 were measured daily on all birds. The method used in all measurements was to place the end of a small ruler at the point of emergence from the follicle and to measure from that point to the tip of the feather. The composite growth curves for these feathers are given in figure 2. All of the points are based on the averages of several birds for each age. The three feathers have similar growth rates, but the proximal ones stop growing sooner. Juvenal primary number 8 does not erupt until the third week after hatching. Numbers 9 and 10 erupt in succession at intervals of about ten days and thirteen days after number 8 emerges.

The first seven greater primary coverts appear at about one week of age followed by the outer two in the third and fourth weeks. Middle coverts emerge in the third week, and the remainder of the upper coverts and all of the under ones erupt later in juvenal plumage development.

At about the same time that primary 10 emerges, number 1 is dropped, marking the beginning of the postjuvenal molt. Subsequently the juvenal primaries through 8 are dropped and replaced by first winter feathers (fig. 1). Juvenal primaries 9 and 10 mature slowly and are not replaced but remain as part of the functional wing through the first winter. Completion of the growth of number 10 in the tenth or eleventh week marks the end of juvenal plumage development.

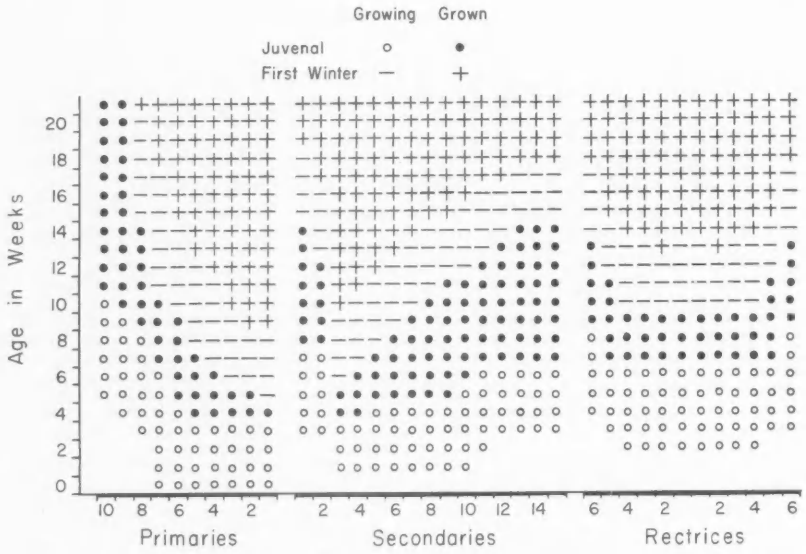

Fig. 1. Summary of postnatal and postjuvenal molts of flight feathers of the California Quail (*Lophortyx californicus*). Method of presentation after Leopold, 1943.

Eight secondaries, numbers 3 through 10, erupt at the age of about one week and the other seven appear in the succeeding three weeks (fig. 1). Both number 1 and number 2, as in the case of the last juvenal primaries to develop, are more like those of the first winter plumage, being plain colored rather than mottled like the other juvenal secondaries. Eight greater secondary coverts erupt at the same time as secondaries 3 through 10, and the other greater secondary coverts erupt at the same time as the corresponding secondaries. Remaining coverts erupt within the following three weeks.

The juvenal alular feathers begin emerging at about ten days of age, the inner one first, then the middle one, and the outer one last, all in close succession. They remain until about the end of the sixth week when they begin to be replaced.

The juvenal rectrices begin to erupt early, the central four pairs emerging nearly simultaneously in the second week. Figure 1 illustrates the general timing of development of this tract. Because of the large amount of wear on the rectrices of these caged birds and because of the occasional accidental plucking of rectrices in handling birds, a detailed analysis of tail feather growth was not possible.

The growth of the body plumage is somewhat complex, each tract developing according to a particular pattern and schedule. Figure 3 summarizes this development by showing the areas of the body that are covered by juvenal feathers at successive intervals during development. Small, isolated patches of pinfeathers appear in the second week on the upper flanks, upper thighs, and scapular area. These patches expand and coalesce with each other and with new centers above and below the tail, and by the fifth week nearly the entire body is covered by juvenal plumage except for the head, which still bears natal down. The down on the head becomes completely replaced in the seventh week.

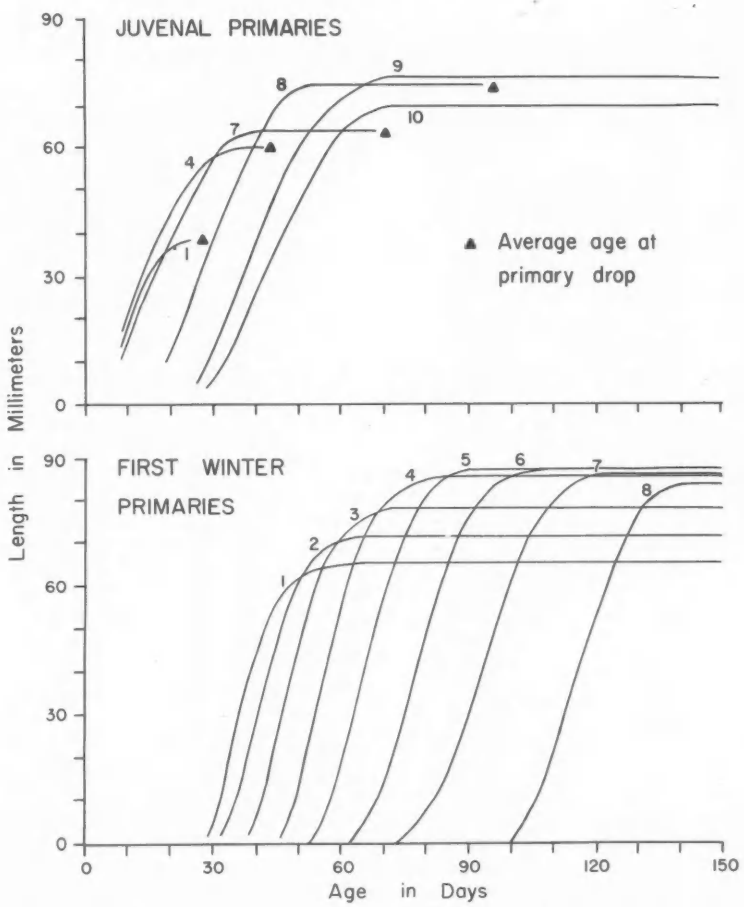

Fig. 2. Growth of individual primaries of California Quail. Each curve is based on mean lengths of several individuals.

FIRST WINTER PLUMAGE

The first winter plumage, which is attained during the postjuvenal molt, is similar to that of the adult and is retained until the first postnuptial molt. With the dropping of juvenal primary number 1 on about the twenty-eighth day, the postjuvenal molt begins. Development of the first winter plumage is not completed until about 24 weeks of age. Thus, the full period required for development is over 19 weeks, as opposed to the ten-week period of juvenal plumage growth.

As in the study of the development of the juvenal plumage, most emphasis in the study of growth of the first winter plumage was given to the remiges, particularly the primaries. Composite growth curves were obtained for all of the primaries (fig. 2). In

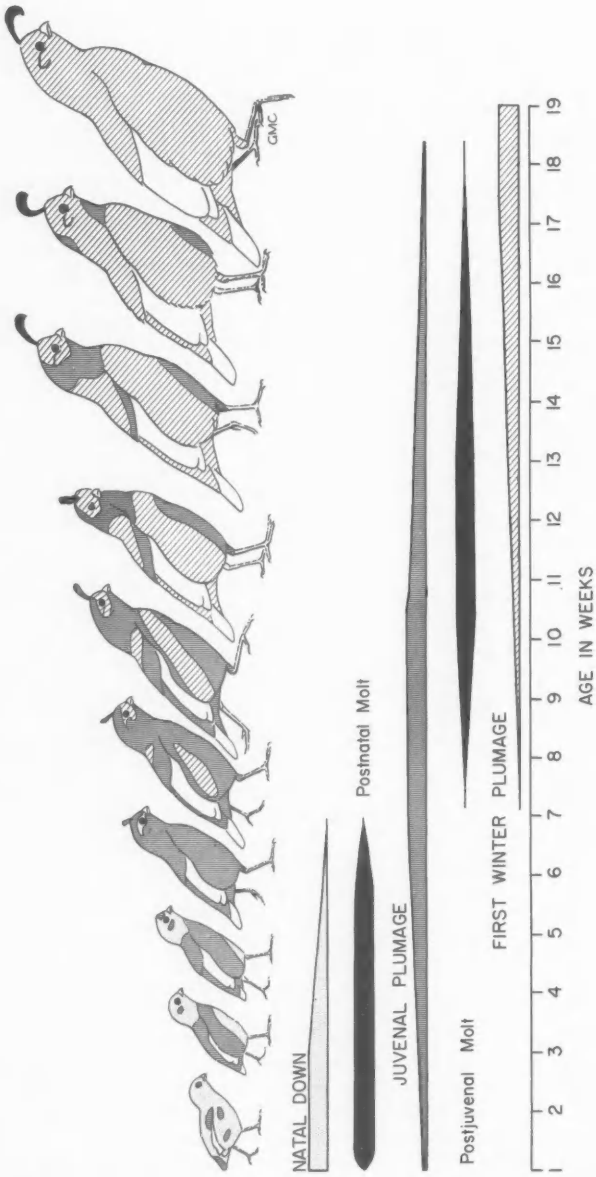
GMC
NATAL DOWN
Postnatal Molt
JUVENAL PLUMAGE
Postjuvenal Molt
FIRST WINTER PLUMAGE
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
AGE IN WEEKS

Fig. 3. Development of body plumage of California Quail. Stippling indicates areas bearing natal down; vertical hatching, areas covered by juvenal feathers; oblique hatching, areas covered by first winter plumage.

general the middle portions of the curves are based upon more individuals and are more likely to be typical. The complete curves available for these feathers are all of a roughly sigmoid shape, which is typical for growth curves in general. The growth rates of the eight first winter primaries are very similar, with a slight decrease in rate in the later ones. The interval between the molting of the successive primaries lengthens progressively from a period of about four days between numbers 1 and 2 to one of over 20 days between numbers 7 and 8.

The program of primary molt illustrated in figure 2 agrees in general with that of Williams (1959:204–205), except with regard to the growth rate of number 8. His figure 1 indicates a markedly lower growth rate and a concomitantly greater age for completion of primary development—25 weeks as opposed to 21 weeks in the present study. Although the curve for primary 8 is based on only seven birds, there is high uniformity within the sample, only ten days separating the two extremes in age of completion of growth. Furthermore, Genelly (*op. cit.*:281), using 19 known-age California Quail, found an average age of completion of growth of number 8 to be slightly over 21 weeks. Williams' curve is based on a comparable sample of 21 birds. Hence, it appears that there may be a real difference in the rate of development between California and New Zealand populations of this species.

There are 15 feathers in the secondary series of the first winter plumage. As in the juvenal series, number 3 is the first to erupt. Number 2 emerges at about the same time as number 11, and numbers 1, 13, 14, and 15 erupt after number 12 (fig. 1). The intervals between the eruptions of secondaries 3 through 10 are five to seven days. Numbers 11 through 15 erupt in rapid succession after number 10. These innermost secondaries are much shorter than the others, except number 1 which is nearly the last to erupt and is the last to complete its growth. It is shorter than the other more distal ones, and its growth rate appears to be slower. With the attainment of full length by number 1 at about 130 days of age, secondary development is completed; this is only shortly before the completion of primary growth.

Petrides and Nestler (*op. cit.*:777) report that, in Bobwhites, secondary number 1 (axial) is not completely grown until two to seven days following full primary growth. Thus, although timing of the primary molt is quite similar in the two species, the secondary molt in the Bobwhite starts at a slightly greater age and requires more time than in the California Quail. This difference is the only significant one discovered in comparison of plumage development of the two species.

The greater primary coverts of the juvenal plumage are not molted but are retained throughout the first year just as are the outer two primaries. These coverts, the first seven of which are mottled brown in color in contrast to the plain gray of their adult counterparts, provide the most obvious and reliable means of separating first-year birds from adults. The greater secondary coverts of the first winter plumage erupt along with the secondaries. The middle and lesser coverts develop in turn after the greater coverts are in, those of the primaries preceding those of the secondaries. The under wing coverts develop last.

In the seventh week the inner juvenal alular feather is molted, and the new, first winter replacement begins its growth. About a week later the middle feather follows suit. The third molts in about 12 weeks, and by 15 weeks of age the alular development is complete.

The order of tail molt is again centrifugal in the postjuvenal molt, and the number of rectrices, namely 12, is the same as in the juvenal plumage. The central four pairs of first winter rectrices appear in rapid succession at about ten weeks of age, and the

outer pair erupt at about 14 weeks. The completion of development is reached by about 18 weeks.

The development of the first winter body plumage follows much the same course as does that of the juvenal body plumage, except that the head begins to molt at the beginning of the sequence. Various stages in this development are illustrated in figure 3. Whereas the juvenal body plumage requires five weeks to complete its growth, the first winter body plumage develops from the age of seven weeks to beyond the age of 23 weeks, a total of over 16 weeks.

At the end of the sixth or the beginning of the seventh week of age, first winter feathers begin to appear below the eye. This is the first area in which sexual dimorphism of plumage becomes evident. In the male these feathers are black, and in the female they are brown. Since the juvenal feathers in this area are brown, it is not possible to be certain of the sex of a female until a few days later (in age) than one can sex a male with certainty.

AGE DETERMINATION

The growth curves of figure 2 provide a means of estimating the chronological ages of young California Quail. The drawings of body plumage development (fig. 3) might also be used in age determination, but the growth of the primaries is more regular and is subject to measurement. Because it was felt that the addition of criteria based on the growth of secondaries might increase the accuracy of age determination, growth rates of secondaries were obtained in this study. However, secondary development proved to be somewhat more variable, and therefore less useful in aging than is primary development. Hence, the detailed data are not included here.

Although the timing of the development of the primaries is well correlated with the age of the bird, the correlation is not perfect. Petrides and Nestler (1943:781) report maximum errors in aging, due to deviation from mean lengths of primaries at given ages, of from four days to thirteen days, the magnitude of maximum error increasing roughly with age. They point out that the data indicate that the true ages of a majority of birds will fall within a period of a week in either direction of the indicated age. Thompson and Kabat (1950), using the table of Petrides and Nestler (*op. cit.*), analyzed discrepancies in age indicated by different growing feathers on the same wing and variation in indicated age of birds of the same brood. This work on wild birds revealed a standard deviation in error of aging of about two days, a variation less than that found by Petrides and Nestler on captive quail.

Wallmo (1956) finds a similar degree of accuracy in Scaled Quail by comparing intervals indicated by primary molt with known intervals in individual wild birds retrapped after varying periods. Using this method and also that of comparing true age with age indicated by primaries in captives of known age, Williams (1959) obtained results agreeing with the others cited.

In this study, deviations of the age indicated by various remiges from the actual known age were ascertained in order to obtain a measure of the reliability of the curves of figure 2 as aging criteria. Ages were chosen that would make use of the middle portion of each growth curve because these portions are probably more nearly true reflections of the samples.

The maximum amount of error in the use of primaries for aging was as follows: juvenal number 1, two days; juvenal 4, four days; first winter 1 and 2, three days; first winter 3, five days; first winter 4 and 5, four days; first winter 6 and 8, eight days; and first winter 7, nine days. Thus, the curves of figure 2 provide a standard for aging which are accurate to within four days up to the age of 70 days and to within nine days

up to 125 days of age. This degree of accuracy is approximately that found by the other workers on age determination in quail.

Another fact emerging from the study of the deviations in apparent age from true age is that individuals tend to deviate in the same direction at various ages. Of the 14 birds used, ten showed a significant departure (by chi square test) from an equal amount of positive and negative deviation. Thus, if a bird were slow in development at one age, it tended to be slow at a later stage, and the same was true for birds tending to be ahead of average development. Therefore, it is doubtful whether accuracy of aging can be increased by using growth stages of more than one primary at a time, as all primaries of any one bird tend to give similar errors as to true age.

The first winter secondaries are more variable in their growth than are the primaries. The maximum range in age of eruption of primaries is 11 days (primary 6). The minimum range in secondaries is 11 days and the maximum is 21. Thus the primaries provide the most reliable criteria of age, and the analysis of variation in aging was confined to them.

Although the growth of primary number 8 is nearly complete at 130 days and the curve is no longer accurate for age determination, the presence of a portion of the growing sheath at the base of this feather indicates an age of less than 145 days and may be used to estimate roughly the age of birds at 20 and 21 weeks. Growing contour feathers may be detected on the medial surfaces of the legs after the sheath of primary number 8 has disappeared. Presence of such feathers denotes an age of less than 165 days.

ADULT MOLT

Adults, including birds at the end of their first year, undergo a complete molt at the end of each breeding season. The course of this molt is regular and similar to that of the postjuvenal replacement.

Dwight (1900) reports a prenuptial replacement of feathers in the facial area in addition to the complete postnuptial molt; however, examination of about 30 museum skins collected in late winter and early spring failed to confirm the existence of this prenuptial molt. Live birds in the study area were not checked specifically for prenuptial molting, but many birds were handled during this period and no molting was noted. At any rate there is but a single complete, or nearly complete, molt each year, the postnuptial molt.

Data on the annual molt were obtained from examination of birds captured in the regular trapping program. Since the molt of the entire plumage is included in the period of primary replacement (Genelly, 1955:281), the lengths of growing primaries were estimated or measured on each molting bird in order to obtain an index as to the extent of molting. Thus, in the primary molt series there are ten major stages corresponding to the dropping of the ten primaries. For each primary, substages may be recognized, according to the amount of growth. In all, forty stages were used in this study, four for each primary; these are plotted against a time scale in figure 4. Males and females are plotted separately. The males begin molting earlier than the females, but the two groups complete the molt at about the same time. These findings agree with those of Genelly (*op. cit.*:282) as to timing and differences between the sexes.

In pheasants, Kabat, Thompson, and Kozlik (1950) found that there is a similar lag of about one month in the beginning of molt in hens as compared to the beginning of molt in cocks. They found that the individual hens molt at the same time as their chicks and they believe, therefore, that hens do not begin to molt until after their broods hatch. Genelly (*loc. cit.*) gives evidence for a similar situation in California Quail. In the pres-

ent study hatching occurred late in 1956, and the molt of the hens was likewise later than in other years. However, the timing of the molt in cocks was similar in all four years. Thus, the situation in pheasants, with the males molting at a regular time each

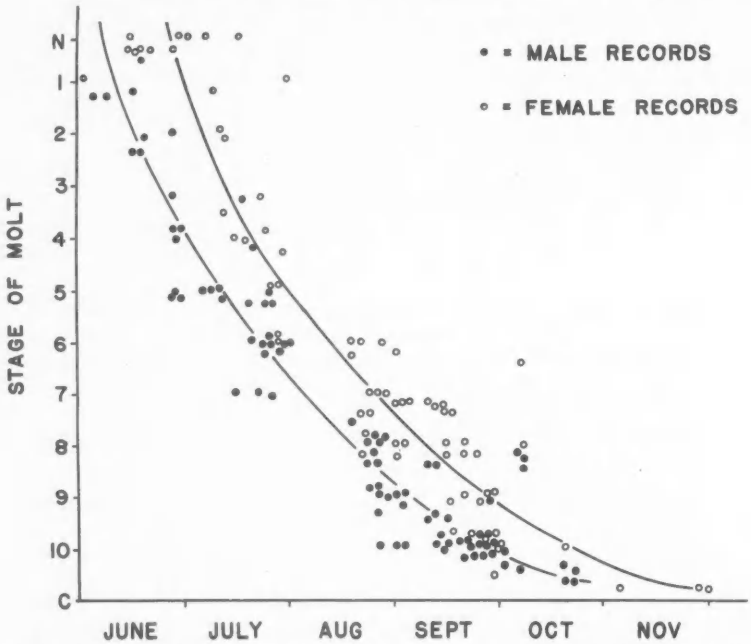

Fig. 4. Timing of adult molt in California Quail. Data from four years are combined. Each circle represents one molting bird. Stages of molt correspond to the number of the primary last molted. The letter "N" signifies that molt had not begun; "C" signifies molt completed.

year and the females not molting until their clutches are hatched, is apparently duplicated in this population of California Quail.

The convergence of the two curves of figure 4 suggests that females molt more rapidly than males. Genelly (*loc. cit.*) found a similar convergence but was not able to conclude whether or not individual females actually complete their molt in a shorter time than individual males. The recapture of various birds of each sex several times during the period of molt in this study has made it possible to estimate roughly the time required for the individual bird to replace its plumage completely. These data indicate that males take over a month longer to complete the molt than do females.

SUMMARY

Young California Quail (*Lophortyx californicus*) are hatched with a covering of natal down. This down is replaced in a regular sequence by the juvenal plumage during the postnatal molt. Juvenal plumage development lasts from the time of hatching until the age of about 11 weeks. The juvenal plumage is replaced by the first winter plumage during the postjuvenal molt, which commences at the age of four weeks. The first winter plumage is fully developed by the age of 21 to 23 weeks. The greater primary coverts

and primaries 9 and 10 of the juvenal plumage are retained for about a year and are molted in the first postnuptial molt. The sequence of feather replacement is similar in all molts except that the head plumage is replaced late in the postnatal molt whereas the head begins molting early in the postjuvenal, and presumably in the postnuptial, molt.

The regular replacement of the series of remiges, especially the primaries, may be used as a gauge to determine the age of the young quail.

Adult quail undergo one complete molt each year at the end of the breeding season. The adult males begin to molt early in June, and the females follow about a month later. Inception of molt in individual hens is apparently governed by the hatching of their young. Females replace their plumage in a shorter time than do males; both sexes complete the molt in late October.

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SOME BIOMETRIC STUDIES ON THE ALBATROSSES OF MIDWAY ATOLL

By Hubert Frings and Mable Frings

Few species of birds have been subjected to such intensive observation as have the Black-footed Albatross (*Diomedea nigripes*) and the Laysan Albatross (*D. immutabilis*) which come to Sand and Eastern islands at Midway Atoll to breed. The result has been the accumulation of a large body of information about their behavior. Yet little of this is quantitative, so that precise information about most phases of their life is lacking. While studying the acoustical behavior of these birds from October 25 until December 14, 1958, we were able, at the same time, to make some quantitative studies of populations and to obtain some biometric data. These do not represent a unified set of observations nor are they part of any overall plan, but they do supply some much needed basic information on the birds.

ARRIVAL OF ALBATROSSES AT MIDWAY ATOLL

The albatrosses come each year from their wanderings over the Pacific Ocean to Midway for breeding in late October and early November. They remain until the following July or August, and then they and their offspring leave. While this general pattern has been well documented and some quantitative data on incubation periods are available, few exact data exist concerning dates of arrival, egg laying, or departure. Bailey (1952, 1956), Hadden (1941) and Chisholm (1937) give some information on time of arrival of the birds, but mostly they refer to "first" arrivals, with only scattered references to population increase. None of the information is quantitative.

To study the course of arrival of the albatrosses at Midway, we censused the birds in selected areas on Sand Island from October 31 until December 8, 1958. Before October 31, there were only scattered sightings. By December 8, the populations had been stable for more than two weeks.

The first Black-footed Albatross was sighted on October 15 and the first Laysan Albatross on October 27. These dates should be reliable, for the men stationed on the island wager on the first sightings, and thus they keep a close watch. On October 26, a survey showed only about 10 Black-foots on the island as a whole, and on the next day there were about 100. They had increased, by October 31, to about 400. Only 10 to 15 Laysans were present at that time.

For censusing we selected six areas, totalling 472,000 square feet, near the beaches where the Black-foots were known to nest regularly, and 22 areas, totalling 672,000 square feet, where Laysans were known to nest. For the Laysans, some areas were chosen especially to give data on the effects of human disturbances, such as earth movements or construction, on the populations. There were eleven areas that had been undisturbed for at least two years, and eleven which had been subjected to disturbances within the previous year. Of the so-called undisturbed areas, only one was not near houses or other buildings. The word undisturbed, therefore, does not mean that these areas had not been altered by man. Probably every square inch of surface on Sand Island had been disturbed in the last ten years.

To study the effects of type of ground cover on populations, seven areas were selected so as to include sections with scattered ironwood trees (*Casuarina equisetifolia*) and adjacent sections with no trees. In the "undisturbed" areas, the ground was covered with grasses, both under the trees and in open parts. In the "disturbed" areas, the grass was just returning after the disturbances and was usually sparse and scattered.

All the birds on the ground in these areas were counted, generally every day at ap-

proximately the same time (4 to 6 p.m.). Kenyon *et al.* (1958) studied the daily cycles of activity and found that flying was especially prevalent in the mornings, thus reducing ground counts. Our casual observations supported this. In a few cases, in which counting was attempted earlier than usual in the day, the counts were lower than usual.

Table 1 presents the data on population build-up for the two species.

TABLE 1

POPULATIONS OF BLACK-FOOTED AND LAYSAN ALBATROSSES IN SELECTED AREAS ON SAND ISLAND[1]

Date	Black-footed	Laysan	Date	Black-footed	Laysan
Oct. 31	26		Nov. 20	666	1385
Nov. 1	233	2	Nov. 21	673	1397
Nov. 2	278	3	Nov. 22	687	1316
Nov. 3	259	4	Nov. 23		
Nov. 4	251	6	Nov. 24	619	1317
Nov. 5	369	8	Nov. 25	705	1521
Nov. 6	357	14	Nov. 26		1518
Nov. 7	419	90	Nov. 27		
Nov. 8	539	139	Nov. 28	631	1560
Nov. 9	496	171	Nov. 29		
Nov. 10	*	190	Nov. 30	603	1551
Nov. 11	428	348	Dec. 1		
Nov. 12	600	597	Dec. 2	541	1525
Nov. 13	519	752	Dec. 3	*	
Nov. 14	566	779	Dec. 4		
Nov. 15	559	894	Dec. 5	424	
Nov. 16		991	Dec. 6		
Nov. 17	499	1044	Dec. 7		
Nov. 18	482	1109	Dec. 8		1548
Nov. 19	648	1133			

[1] Total census areas: Laysan, 672,000 sq. ft.; Black-footed, 472,000 sq. ft.
* Unauthorized killing in census areas; there was also disturbance in the areas with Black-foots from November 15 to 16.

In the Black-foots, the population increased slowly for the first two weeks, October 15 to 31. Thereafter, the increase was rapid but irregular until about November 8, after which there was a slow increase. The population was stable by about November 19. Twice during the time of arrival about 200 Black-foots were killed without authorization in two of the census areas, as indicated in table 1, and further harassments occurred in the areas on November 15 and 16. Thus, the date for final stability found here may be somewhat later than it would have been under untroubled conditions. However, there is no doubt that about one month elapsed between arrival of the first bird and stabilization of the population. This is a considerably longer time than the reports of Hadden (1941) and Bailey (1952) would lead one to suspect.

For the Laysan Albatrosses, likewise, the population increased only slowly at first, from first arrival on October 27 until about November 7. After this, the increase was rapid but irregular for about two weeks, followed by a slow increase. The population was relatively stable by about November 25. These data, again, show a much longer time of arrival than Bailey's (1952) statements suggest, but they agree with Hadden's estimates fairly well.

Hadden (1941) states that male Laysan Albatrosses return first and implies that the females arrive about one to two weeks later. He does not indicate how he distin-

guished the sexes, but it is possible that he did this by observations on behavior. Bailey (1952) recounts Hadden's information but incorrectly states that the dates are for Black-foots, thus making it seem that, in both species, the males return first.

We had the opportunity to study this by determining the sexes of the birds that were accidentally killed by collision with objects on the island or by automobiles on the roads. There was no evidence, when we knew that both sexes were present in about equal numbers, that accidental deaths were more frequent in one sex than in the other. These samples, therefore, probably gave a good estimate of the relative numbers of males and females present.

For the Black-foots, there was no evidence that males arrived significantly before females. At all stages, except possibly before October 31, when only a small part of the population was present, males and females were found in about equal numbers. On the contrary, for the Laysans there was a striking preponderance of males over females between November 1 and November 15. After that the proportion of females rose, and after about November 20 the sexes were found in approximately equal numbers. Thus, Hadden's statement for the Laysans is confirmed, but the extension of this to Black-foots seems to be incorrect.

The general picture of arrival of the albatrosses at Midway would thus seem to be as follows. The Black-foots arrive about 10 to 14 days before the Laysans. The first Black-foot appears from October 15 to 20, and the first Laysan from October 25 to November 1. For 7 to 10 days after the arrival of the first bird, very few appear. After this, for 10 to 14 days, a rapid but irregular increase occurs, after which the rate of increase diminishes. Stable populations are reached 5 to 10 days thereafter. The Black-foots seem to be fully settled by November 15 to 20, the Laysans by November 23 to 27. For the Laysans, males arrive before females; approximate equality of the sexes in the population is achieved when the population has become almost stable. For the Black-foots, however, both sexes seem to arrive in about equal numbers throughout.

HABITAT PREFERENCES

It is well known that the Black-foots prefer open sandy areas usually near the sea for their nests, whereas the Laysans prefer sheltered areas with some growing vegetation. Most of the plants on Sand and Eastern islands of Midway Atoll are introduced species, and their distribution is determined chiefly by man's activities. Accordingly grasses and ironwood trees are maintained best near houses and other buildings. The Laysan Albatrosses, therefore, tend to congregate for nesting in the housing areas on Sand Island and at places on both islands where man's activities have resulted in the presence of grass and thin stands of trees.

The disturbances to which the islands have been subjected have had profound effects on the local populations of Laysan Albatrosses. This can be seen in table 2, in which the populations of Laysans, at the time of stability, are given for areas with different types of ground cover and histories. The terms, disturbed and undisturbed, were defined previously. The preference for partly tree-covered, grassy areas is obvious. It is interesting to note that trees in recently disturbed areas greatly increase the carrying capacity of these areas. The area described in table 2 as "dense thicket and dunes," was probably as nearly wild as could be found on Sand Island. This was landward of the dunes in an area little disturbed or traversed by man. The dominant plant was *Scaevola frutescens*, a native shrub forming dense thickets between which there were small sandy areas with scattered grass. It is clear that such a situation does not support as dense a population as does a grassy area with scattered trees. Man's predilection for grass and shade trees on these islands seems to have very definitely favored the Laysan Albatross.

TABLE 2

NUMBERS OF LAYSAN ALBATROSSES IN VARIOUS TYPES OF HABITATS IN SELECTED AREAS ON SAND ISLAND, NOVEMBER 26 TO 30, AND AVERAGE AREAS IN SQUARE FEET OCCUPIED BY EACH BIRD

Habitat types[1]	Areas	Nos.	Sq. ft./bird
Undisturbed			
Open, grassy	71,000	315	225
Tree-covered, grassy	95,000	746	127
Disturbed			
Open, scattered grass	447,000	309	1450
Tree-covered, scattered grass	45,000	152	296
Dense thicket and dunes	14,000	45	311

[1] "Disturbed" and "Undisturbed" refer to disturbance by construction or earth movement by man within 2 to 3 years.

The maximum populations of the Laysan Albatross found at Midway Atoll occurred on Eastern Island in particularly favorable areas, such as near the old terminal building. Here recent human interference was minor, and grassy ground cover and scattered trees and bushes remaining from former use by man created apparently optimal conditions for nesting. To learn how many Laysans might be accommodated under these conditions, the nests and the distances from each nest to its neighbors were measured.

The mean diameter to the outer edge of the "moat" around the nest for 63 individuals was 39 ± 0.26 inches (99 ± 0.66 cm.). The range in size was from 34 to 44 inches (86 to 112 cm.). The mean distance from edge to edge of neighbor's nests, based on 190 measurements, was 26 ± 1.3 inches (66 ± 3.3 cm.). The range was 0 to 72 inches (0 to 183 cm.), the median 21 inches (53 cm.). These figures give about 24 square feet per nesting pair (2.23 $m.^2$) for the Laysans. The most densely populated area studied on Sand Island was that across from the Station Hospital, and here the area per bird was 70 square feet. Considering that trees and other objects made nesting impossible on about one-third of this area, one can consider it to be nearing the saturation point.

It is obvious from the data on populations in areas disturbed by man's activities that statements that the albatrosses at Midway are resisting man's encroachment are not true. As we have shown (Frings and Frings, 1959*b*), the populations of both Blackfoots and Laysans on Sand Island are falling under man's harassment. The campaign under way to denude and level the dunes, while of questionable value in deterring flight over the runways, is certainly going to force many birds off the island. For the maintenance of the populations of these species at levels sufficient to forestall any danger of depletion, it would seem that improvements on Laysan and Lisianski islands to bring their carrying capacity nearer to the optimum than it is now are justified and indeed advisable. The present populations of these islands (Kenyon *et al.*, 1958; Rice, 1959) are far short of those that could be supported under even sub-optimal conditions (Frings and Frings, 1959*b*).

WEIGHTS OF ALBATROSSES

There are in the literature only scattered and non-quantitative references to the weights of these birds. To obtain information on this point, individuals that were killed accidentally on Sand Island were collected daily and were weighed and dissected for study of fat reserves and reproductive cycles. The data on weights are presented, in part, in table 3.

From November 12 to 16, most of the females still had eggs in the oviducts; from November 26 to December 3, most had laid eggs. The data presented thus allow comparison of the weights before and after egg laying. It is interesting to note that although

TABLE 3

WEIGHTS IN KILOGRAMS OF BLACK-FOOTED AND LAYSAN ALBATROSSES AT TWO TIMES DURING NESTING AND EGG LAYING

	November 12 to 16			November 26 to December 3		
	N	Range	Mean $\pm \sigma_m$	N	Range	Mean $\pm \sigma_m$
Black-footed						
♂ ♂	123	2.6–4.3	3.40±0.032	45	2.3–3.6	3.12±0.036
♀ ♀	104	2.6–3.6	2.99±0.027	34	2.2–3.3	2.76±0.059
Laysan						
♂ ♂	152	2.7–4.1	3.31±0.023	81	2.4–3.9	3.08±0.032
♀ ♀	54	2.5–3.6	2.99±0.036	80	1.9–3.3	2.76±0.036

the males in each species are significantly heavier than the females, the differences between the weights of the same sexes of the two species are not significant. Earlier workers often implied, without quantitative data, that Black-foots are heavier than Laysans, and we found (Frings and Frings, 1959*a*) this to be the case for a few individuals which were sent to us in Pennsylvania in April, 1958.

All the birds, up to the time of our leaving Midway had extensive deposits of fat. It is possible that the weight of this excess fat, which was being consumed as incubation progressed, masked any difference in weight between the two species. At any rate, from the time of arrival until mid-December, the two species had similar weights; in both species, the males were about 0.4 kg. heavier than the females.

DETERMINING THE SEXES OF THE ALBATROSSES

The sexes in these species are almost identical externally. Actually, except for fortunate observations during critical behavior periods, it is almost impossible to distinguish the sexes of living individuals with certainty. Hadden (1941) implied that he could distinguish between the sexes, but he gave no hint as to how he did this.

In general, as shown in table 3, the males are heavier than the females, and Loomis (1918) found, for Black-foots, that males are larger, as determined by length, depth, and width of bill and length of tail, wing and tarsus. These, however, were not suggested as means for distinguishing sexes in the field.

Starting with a suggestion that the heads of males looked "flatter" ("as if with a 'crew-cut'") than those of females, we used the dead albatrosses, which could be sexed by dissection, to measure the width, depth and length of the head and the length and and depth of the beak. All of these showed a sex difference, the males being larger. However, measuring the length and depth of the head and the depth of the bill proved to be difficult to do consistently, and the measurements of males and females overlapped considerably. We shall, therefore, omit consideration of these here. Measurements of head width and bill length afforded the required tool for sexing, and the data on these will be presented.

The head width was measured, using dividers and ruler, on the dorsal side at the widest point, just behind the eyes. At this point on each side, the skull has a blunt angle which is easily palpated. We found it best to have one person make all the measurements, for the skin can be variably compressed by different persons. The length of the bill was measured from the angle of the mouth to the tip. Again, variations in pressing back the feathers at the base resulted in some variation in measurements among different persons, and so only one person performed all the measurements. The absolute values

TABLE 4

HEAD WIDTHS OF BLACK-FOOTED AND LAYSAN ALBATROSSES AND THE RATIOS OF MALES TO FEMALES WITH HEAD WIDTHS THE SAME

Head width (mm.)	Black-footed ♂♂	Black-footed ♀♀	Black-footed Ratio ♂/♀	Laysan ♂♂	Laysan ♀♀	Laysan Ratio ♂/♀
53					1	
54		1			6	
55		5			22	
56		10		3	32	1/11
57		18		8	32	1/4
58	2	28	1/14	30	12	2.5/1
59	7	23	1/3	33	4	8/1
60	13	7	2/1	28	3	9/1
61	18	1	18/1	21		
62	24			2		
63	12			3		
64	2			1		
65	1					
Totals	79	93		129	112	
Means	61.3	57.8		59.3	56.4	
σ_m	0.16	0.15		0.13	0.13	
*d/SE_d	15			16		

* d/SE_d = difference between means of males and females divided by the standard errors of the differences.

in tables 4 and 5, therefore, should not be used directly by anyone else. It is necessary, if the differences between males and females are to be determined accurately, to develop one's own standard procedures. When this is done, these measurements allow one to determine the sexes of living Black-footed and Laysan albatrosses with a high degree of certainty. The sex differences for each species in these measurements are obvious: the males are consistently larger. Black-foots have significantly wider heads than the corresponding sexes of Laysans; Laysans have longer beaks.

Using these data, one can construct tables of measurements for determining sexes of the birds. Thus, for Black-foots, all individuals with head widths of 57 mm. or less are females, and all with head widths of 62 mm. or over are males. On these bases, 42 per cent of the birds can be assigned to the correct sex with certainty. Between 58 and 61 mm., one can set up probabilities, as indicated in table 4. At 58 mm., the chances are 14:1 that the individual is a female, and at 61 mm., 18:1 a male. These figures may be considered as indicating a high degree of probability, and thus give another 29 per cent at high probability, a total of 70 per cent of the population. For the Laysans, 23 per cent can be sexed with certainty from head widths and a total of 69 per cent can be sexed with probabilities of 8:1 or better. Correspondingly, for bill length in Black-foots, 52 per cent have lengths of 93 mm. or less and are thus females, and those with lengths of 100 mm. or more are thus males; another 18 per cent have measurements of 94 to 95 mm. and are thus indicated to be females at probabilities of 11:1 or better. Similarly for Laysans, one can determine 40 per cent certainly and a total of 75 per cent at odds of 25:1 or better.

The level of correlation between head width and bill length in individuals is sur-

TABLE 5

BILL LENGTHS OF BLACK-FOOTED AND LAYSAN ALBATROSSES AND RATIOS OF MALES TO FEMALES WITH BILL LENGTHS THE SAME

Bill length (mm.)	Black-footed ♂♂	Black-footed ♀♀	Black-footed Ratio ♂/♀	Laysan ♂♂	Laysan ♀♀	Laysan Ratio ♂/♀
86–87		2				
88–89		6				
90–91		14				
92–93		26			1	
94–95	3	33	1/11		6	
96–97	11	23	1/2		7	
98–99	21	6	3.5/1		22	
100–101	21				23	
102–103	22			2	49	1/25
104–105	10			20	22	1/1
106–107	3			36	6	6/1
108–109				51	1	51/1
110–111				33		
112–113				23		
114–115				5		
116–117				2		
Totals	91	110		172	137	
Means	100.5	93.7		108.7	101.4	
σ_m	0.28	0.25		0.21	0.25	
d/SE_d	18			22		

prisingly low. For male Black-foots the correlation coefficient (r) is +0.14, and for females it is +0.21. For male Laysans it is −0.06, and for females it is +0.11. These two measurements should be useful almost independently, therefore, and so they proved to be. The following summary of determinations of sexes for 160 Black-foots and 240 Laysans confirms this point.

	Black-footed	Laysan
Sex certain (one of two measurements in certain range)	87 per cent	70 per cent
Sex determined with combined probability of 15:1 or better	9	17
Sex indeterminate, or with probability of 5:1 or less	4	13

When we had completed measuring about half of those ultimately measured, we constructed the tables and thereafter tested the data by predicting sexes from the measurements before dissection. We were able to be essentially certain of the sexes in about 90 per cent of these tests. In most cases of even small probability, the sex was correctly predicted from the measurements. In no case was the sex indicated to be certainly male or female by one measurement and the reverse by the other.

When we were able to determine sex in this way, we tried estimating sex from the general appearance of the heads: males with flatter appearing heads than females. When two individuals could be seen together, this was not difficult to do correctly. With just one bird, however, it was much more difficult and subject to error. There were some individuals which were so obviously male or female, on the basis of head shape, that they were easy to determine, but many others were not so clear-cut. In general, one could use this sight method for a preliminary estimate of sex, and if this could be sup-

ported by some behavioral observations it might prove valid enough, but it would be best to check by measuring.

SEXES OF DANCING ALBATROSSES

The dancing (ecstatic ritual) of these birds has excited considerable interest, but the interpretation of this behavior is still obscure. While presumably a courtship performance, it is not usual in the colony before egg laying. Earlier workers seem to have tacitly assumed that the dancing individuals—usually two, but by no means always so —were of opposite sex. Unfortunately, these workers gave no reasons for their belief. nor did they indicate how they determined the sexes.

Using head widths and bill lengths, we were able to study this. It was easy to capture both members of a dancing pair. They were measured and released, and then the measurements were compared with the tables previously discussed. The results follow:

	Black-footed	Laysan
Sex of one member, at least, indeterminate	2	16
Dancers certainly of opposite sex	4	55 (66 per cent)
Dancers probably of opposite sex (one member certain; other of high probability)		18 (21 per cent)
Both dancers females		8 (9 per cent)
Both dancers males		3 (4 per cent)

Too few Black-foots were measured to draw any conclusions. It is obvious from the data on the Laysans that most of the dancing pairs, by far, consist of a male and female. However, pairs can be found consisting of members of the same sex. We shall not speculate on the significance of these data in understanding the dancing behavior. Dancing, however, seems to be predominantly a heterosexual performance.

ACKNOWLEDGMENTS

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SUMMARY

The build-up of populations of the Black-footed Albatross (*Diomedea nigripes*) and Laysan Albatross (*D. immutabilis*) during their annual arrival at Midway Atoll for breeding was followed by daily censuses in selected areas. About one month passed from the date of first arrival in each species until the population was stable: Black-foots from October 15 until about November 19; Laysans from October 27 until about November 25. Black-foots prefer open, sandy beaches for nesting; Laysans prefer areas with grasses and scattered trees. Thus the Laysans seem to be favored by man's presence at Midway. Disturbances by man that resulted in reducing ground cover reduced the population of Laysans. During the period of arrival and egg laying, the weights of the two species were essentially the same. Males in each species were about 0.4 kg. heavier than females. By measuring head widths and bill lengths of individuals whose sex was determined by dissection, it was found that males were significantly larger than females in these two dimensions. These measurements could be used to determine the sex of living birds in about 90 per cent of the cases. Using this method for sexing, it was found that individuals performing the albatross dance as a pair were, in 85 per cent of the cases, of opposite sex.

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SOME SEASONAL CHANGES IN MORPHOLOGY OF THE RUFOUS-SIDED TOWHEE

By JOHN DAVIS

Seasonal changes have been demonstrated in a number of avian tissues and organs and in bird weight. Such changes indicate not only seasonal changes in morphology but they may, in some instances, suggest the nature of the morphologic and physiological adjustments made by the individual as it passes from one season to the next. This study is concerned with seasonal changes in bill length, in length of the intestinal tract, or gut, and in weight of a resident race of the Rufous-sided Towhee, *Pipilo erythrophthalmus megalonyx*. Data were derived from samples of males and females collected at, or as close as possible to, two-week intervals near the Hastings Reservation, two and one-half miles east of Jamesburg, Monterey County, California, from January 5, 1955, to May 10, 1956.

Each specimen was autopsied in the field and the gonads were either removed (males) or examined *in situ* (females). Each bird was weighed on return from the field, its intestinal tract was measured, the amount of stored fat was estimated, and the skin was saved. In addition, the stomach contents were examined and a rough estimate was made of their composition.

BILL LENGTH

Skins were stored for a minimum of three months before bill length was measured to allow for possible shrinkage of the bill. Measurements were made from the anterior edge of the nostril to the tip of the bill. In a previous paper (Davis, 1954), seasonal variation in bill length was demonstrated in a number of passerines which change from an almost exclusively vegetable diet in the late fall and winter, when the bill is short, to a diet which includes a prominent component of insect material in the spring and summer, when the bill is long. Such variation was ascribed to the increased wear put on the constantly-growing bill tip by the more abrasive winter diet. Like these other species, the Rufous-sided Towhee shows a similar seasonal change in diet, as indicated by examination of the stomach contents of the specimens collected. In addition, the stomachs of towhees taken in winter contained large amounts of dirt and grit, whereas such material was present in much smaller amounts in the stomachs of birds taken in summer (table 1). The more frequent picking up of such inert, abrasive material in winter may accentuate the wear imposed on the bill tip by the winter diet. In each sex, the bill length of the winter sample is significantly less than the bill length of the summer sample (fig. 1). Thus, the Rufous-sided Towhee shows the same type of diet-correlated seasonal variation in bill length that was demonstrated for the passerines discussed in my earlier paper (Davis, *op. cit.*).

INTESTINAL TRACT

The intestinal tract of each specimen was removed at the gizzard and at the vent, thus including the cloaca. The intestines were freed from their mesenteries and laid along a ruler in as straight a line as could be achieved without stretching. Since the same technique of measuring was used for each specimen, the relation of measurements taken at different times of the year should not have been influenced by the technique. Three measurements were taken: small intestine, from the gizzard to the origin of the colic caeca; large intestine, including the cloaca, from the origin of the colic caeca to the vent; and total length of the entire tract. It should be pointed out that measurements were not taken of the intestines of every specimen, and in some cases only the entire intestine or the small intestine was measured. Thus, sample sizes vary.

TABLE 1

OCCURRENCE OF INERT MATERIAL IN STOMACH CONTENTS

	0	+	++	+++	++++[1]
January	1	4	10	12	
February	1	2	9	9	
March	1	9	6	12	
April	4	15	3	1	
May	5	7	4	....	
June	7	1	....	1	
July	5	4	2	1	
August	....	3	3	7	
September	....	6	4	3	
October	2	5	1	2	
November	....	....	2	8	
December	....	1	2	7	1

[1]Estimated amounts from none (0) to considerable (++++). Data include seven juveniles.

Leopold (1953) demonstrated intergeneric variation in the relative length of the intestinal tract and caeca for several genera of gallinaceous birds. The intestines and caeca were relatively long in browsing genera, which depend on low-quality food sources in winter, and relatively short in seed-eating genera utilizing higher quality winter diets. He also showed that there were similar differences between coastal and interior populations of the California Quail (*Lophortyx californicus*) subsisting on relatively poor and relatively rich diets, respectively. He concluded that greater intestinal length in forms utilizing relatively poor diets allowed for more thorough digestion and perhaps for more complete absorption of the essential elements in the diet.

In this study, it has been possible to demonstrate significant seasonal variation in the length of the gut within a single restricted population of the Rufous-sided Towhee. As can be seen in figure 2, the entire intestinal tract was significantly longer in the winter sample of each sex than in the summer sample. The same is true of the small intestine (fig. 3). The large intestine is significantly longer in winter males but not in winter females (fig. 4). Since the large intestine, as measured, included the cloaca, the lack of significant seasonal variation in the females may reflect sexual dimorphism in the relative proportion of the length of the large intestine to the length of the cloaca.

The greater length of the intestine in winter correlates with the primarily vegetarian winter diet, a diet which would be lower in protein content than the spring and summer diet. Thus, intestinal length appears to be correlated with the relative richness of the diet, agreeing with the findings of Leopold in gallinaceous birds. The longer intestinal tracts of towhees taken in winter apparently allow for a longer period of digestive breakdown of the lower grade vegetable matter which forms most of the food at that season.

Since it is possible to demonstrate significant seasonal variation in intestinal length within a single restricted population of towhees, it seems likely that the difference in intestinal length found by Leopold (*op. cit.*) between coastal and interior populations of California Quail does not represent a genetically controlled interpopulation difference but merely represents the somatic response of the individuals within each population to different diets.

WEIGHT

Linsdale and Sumner (1937:163) present a number of weights for Rufous-sided Towhees live-trapped and weighed repeatedly. Their data are fragmentary and their table 4, which presents the data by months, is most difficult to interpret and does not

make clear how many individuals were involved in the monthly mean weights. Therefore, I am unable to make any direct comparison between their findings and mine.

Weights of males only are considered here, as my samples of females were too small to permit satisfactory analysis. Further, the enormous development of the reproductive

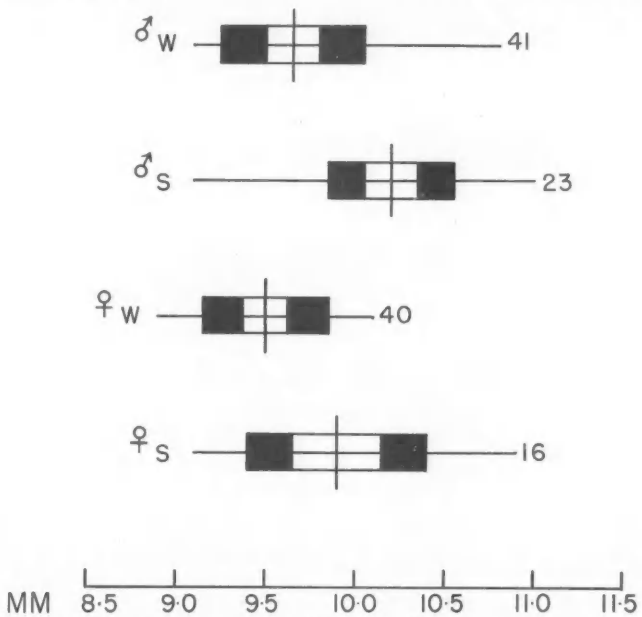

Fig. 1. Seasonal variation in bill length of the Rufous-sided Towhee (*Pipilo erythrophthalmus*). Samples of males are of adults only, samples of females are of adults and of first-year birds collected after December 1. Winter samples (W) were collected from October through April; summer samples (S) from May through September. Sample size is indicated to the right of each diagram. The vertical line represents the mean, the horizontal line the range; the white rectangle equals two standard errors on each side of the mean, the black rectangle one standard deviation on each side of the mean.

tract in breeding females seriously affects weight and makes it impossible to compare the weights of females collected during the breeding season with the weights of females collected at other times of the year. For example, a female collected on April 27, 1956, weighed 48.3 grams, of which 4.4 grams, or 9.11 per cent, was accounted for by the enormously expanded oviduct and the full-size egg, ready to be laid, at the terminus of the oviduct. The ovary, which was not weighed, contained two large, yolky follicles measuring 6 mm. and 12 mm., and it would have accounted for a still further percentage of the total body weight.

Since the testes were removed from each specimen in the field, it should be emphasized that the weights presented in figure 5 are of males without the gonads *in situ*. Specimens were collected purely at random, and such variables as time of day and the amount of time elapsing prior to weighing are minimized. Desiccation of these specimens

autopsied in the field prior to weighing was apparently of no importance, as samples collected in July, August, and September averaged higher than the sample taken in June, although air temperatures were higher in July, August, and September (table 2), and desiccation should have been greater in those months than in June. Conversely, the

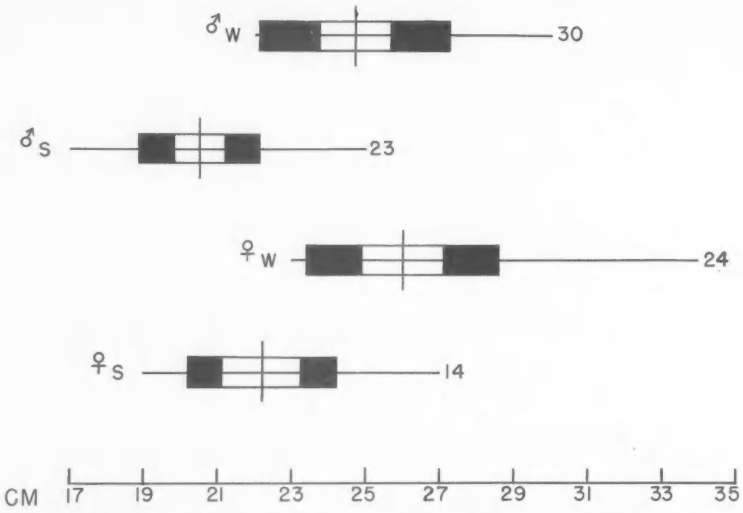

Fig. 2. Seasonal variation in total length of the intestinal tract of the Rufous-sided Towhee. Samples of males are of adults only; samples of females are of adults and first-year birds. Winter samples were collected from September through March; summer samples from April through August.

sample taken in February was considerably lighter than either of the samples taken in December or January, although February was a colder month than either December or January (table 2).

TABLE 2

MEAN TEMPERATURES IN DEGREES FAHRENHEIT FOR 1955 AND 1956

	Maximum	Minimum	Mean
June[1]	78.4	44.0	61.2
July	80.3	47.0	65.1
August	92.4	52.5	72.5
September	88.7	49.8	69.2
December	60.0	39.4	49.7
January	57.0	34.4	45.7
February	59.7	31.2	45.4

[1]January and February temperatures are for 1955 and 1956 combined; all others are for 1955.

The annual weight cycle of adult males is given in figure 5. The greatest irregularity was found between July and November. With the exception of the sample collected in October, the differences among the other four months span a range of only 1.2 grams, and the difference between any two of these four months is undoubtedly not statistically significant. In the period from July through November, weight is probably maintained,

somewhat above the June mean, in nearly straight-line fashion. I cannot account for the marked increase in weight shown by the sample taken in October.

First-year males were considered only from January to May. Samples collected between September and December consistently averaged lighter than samples of adults

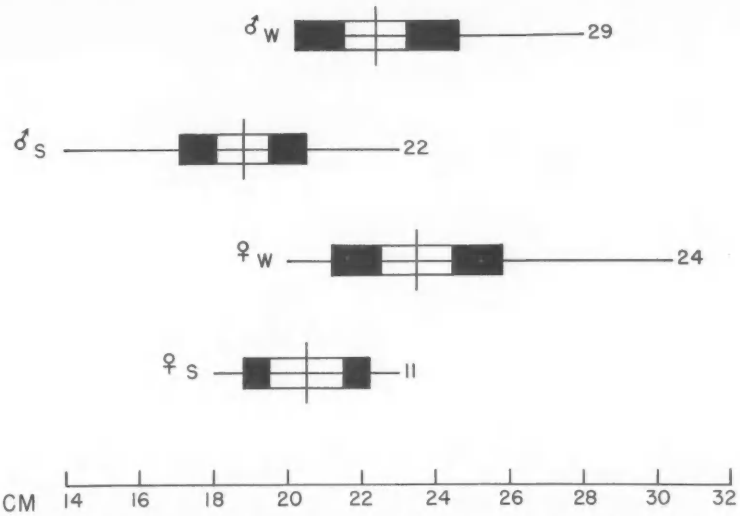

Fig. 3. Seasonal variation in length of the small intestine of the Rufous-sided Towhee. The composition and monthly limits of samples are as for figure 2.

and were not considered. Even the January sample of first-year males averaged 1.6 grams lighter than the sample of adults collected in that month. No first-year male was collected in June. Figure 5 indicates that the samples of first-year males collected between January and May showed a nearly steady decrease in weight which almost exactly paralleled the decrease in adult weight in the same period. The only divergence between the two age groups was found in the samples taken in April and May; the means of these were nearly identical in the adults, but the first-year males showed a further decrease in weight in May. In general, the two age groups show an almost identical pattern of decrease in weight from February to May. That this decrease is significant is indicated by a comparison of the mean weights of adults for the periods from October to January and from February to June, 43.33 ± 0.57 and 40.32 ± 0.33 grams, respectively.

The period of weight decrease from February to June virtually coincides with the breeding season of the males. The first signs of gonadal activity are noted in January, but Leydig cells do not become common in the testes of most males until about the middle of February (Davis, 1958:309, 312). Singing is first heard in late January or early February but it does not become widespread in the male population until mid-February (*op. cit.*:314). Thus, mid-February may be considered the beginning of the male breeding season. Testis regression was first noted in adults between July 6 and 20, but singing becomes less frequent by early July (*op. cit.*:309, fig. 1; 321, table 6). Nesting activities are over for most pairs by the end of June (Davis, 1960:435). Thus, the breeding season of the males comes to an end between early July and mid-July, and it

virtually coincides with the period of almost steady weight decrease from February through June.

It seems most likely that this weight decrease is brought about by one, or both, of two factors. First, it is possible that the change in hormonal balance brought about by

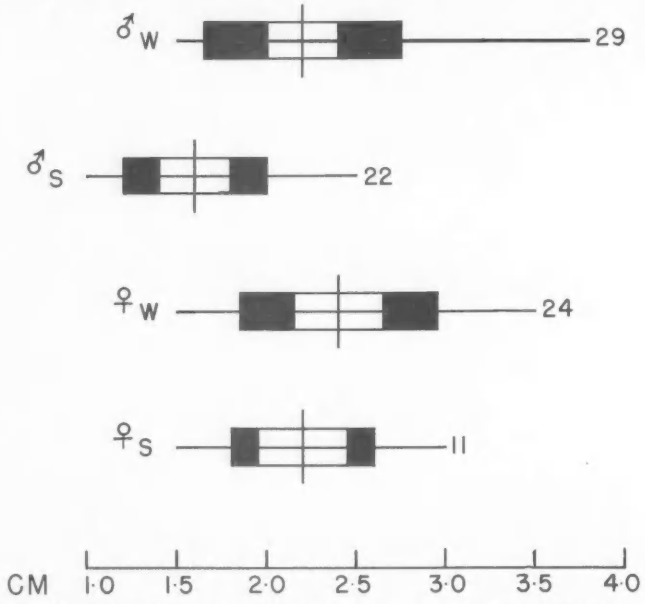

Fig. 4. Seasonal variation in length of the large intestine of the Rufous-sided Towhee. The composition and monthly limits of samples are as for figure 2.

the development of the gonads may account for part of the decrease in weight. Second, the diversion of time and energy from foraging and resting to other activities such as singing, other aspects of territorial defense, and nesting could bring about a decrease in weight during the breeding season. Of the two, the second factor may be the more important. Some idea of the amount of time spent in activities other than foraging and resting during the breeding season is given by the amount of time spent singing by certain individuals. The following data are taken from Davis (1958). An unmated male watched for eight hours on May 24, 1956, spent 84.3 per cent of his time singing. A nesting male watched during the incubation period sang 18.8 per cent of the time on one day and between 30.8 and 45.1 per cent of the time on the remaining eight days of observation; another, watched for seven days during the incubation period, sang from 30.8 to 62.9 per cent of each day. Thus, although the males do not incubate, they do spend considerable time singing. Once the young have hatched, the males sing less, but they spend considerable time gathering food for the nestlings (Davis, 1960). Earlier in the breeding season, considerable time is spent in singing, in patrolling territories, and in active territorial defense. As can be seen, once the breeding season is under way, foraging and resting time is sharply limited and time and energy are spent on a variety of other activities.

As soon as the breeding season is over, the males at once start to gain weight (fig. 5). Of interest is the fact that adult males gained weight throughout the period of molt, which began between July 6 and 20 and ended for most birds in late August or early September.

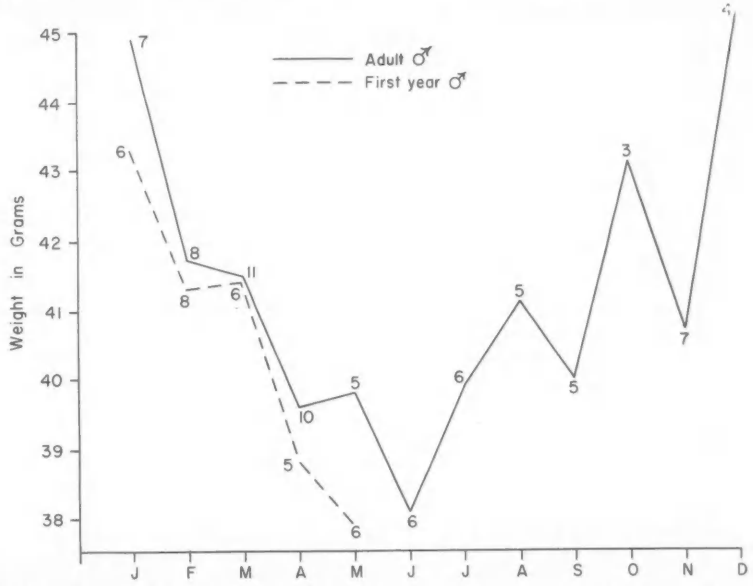

Fig. 5. Mean monthly weights of adult and first-year male Rufous-sided Towhees, weighed after the testes had been removed. Sample size is given by the numeral adjacent to each monthly mean.

Baldwin and Kendeigh (1938:446–448) found a positive inverse correlation between the curve of monthly mean air temperature and a composite curve of mean monthly weight of a wide variety of species. The low point in the weight curve coincided with the high point in the curve of air temperature. No such correlation is evident for the towhees considered in the present study, as the low point in the weight cycle was reached in June, but July, August, and September were all hotter months (table 2). In July and August, mean monthly weight increased, and although it fell somewhat in September, it remained above the June low. The highest mean weight was found in the combined samples of December, 1955, and January, 1955 and 1956. The combined samples of February, 1955 and 1956, were noticeably lower in weight (fig. 5), yet average temperatures were lower in February than in December and January (table 2). Therefore, it is not possible to find any correlation between average monthly temperatures and mean monthly weight.

Seasonal variation in weight cannot be accounted for on the basis of seasonal variation in fat deposition. The amount of fat present in 77 adult male specimens was estimated, after skinning, as none, slight, moderate, or heavy. Of these 77, 69 were classed as having no fat or slight fat. The remaining eight were classed as moderately fat. Four of seven collected in January were so classed, as were two of nine collected in February,

one of five collected in August, and one of three collected in October. January was the only month in which there was a marked tendency toward fat deposition. Of 40 first-year males collected from September through May, 38 were classed as having no or slight fat, and two of seven collected in January were classed as moderately fat. Again, January was the only month in which there was any evidence of a tendency to deposit fat.

Of the 64 adult and first-year females for which data on stored fat were recorded, only eight were classed as having moderate or heavy deposits of fat, as follows: three of ten collected in January; one of seven collected in April; three of four collected in October; and one of five collected in December. In the females there appeared to be two months in which fat was deposited, October and January.

The preponderance of fat birds in the October sample may have some relation to the sharp rise in the mean weight of the October adult males, although only one of three adult males collected in October showed even moderate deposits of fat. The only month in which some individuals of all four age-sex groups showed moderate to heavy fat deposits was January. With the exception of two females, one collected on January 18, 1956, and one collected on October 24, 1955, both with heavy fat deposits, no individual had more than moderate amounts of stored fat. In December, when the mean adult male weight was slightly higher than the mean for January and represented the greatest mean weight for any month, only one bird, a first-year female, of 11 representing all age-sex groups, was even moderately fat.

One must look for sources of weight loss other than consumption of stored fat to explain the significant difference between the mean weights for the periods of October to January and February to June in adult males. Three such sources are suggested to explain at least a part of this difference.

First, the adult males were weighed without the gonads in place. An adult male collected in May, 1960, had testes which measured slightly smaller than the testes of known breeding males which had been examined microscopically. The testes of the bird collected in 1960 weighed, together, 0.4 grams. On the basis of measurements, the testes of other, known breeding birds would have weighed slightly more, perhaps 0.5 grams. Thus, one would be justified in adding about 0.5 grams to the mean weights shown in figure 5 for the months of April, May, and June, when the testes were at, or near, full size. In other words, approximately 0.5 grams of the weight difference between the high and low points of the cycle might be accounted for on the basis of the growth and development of the testes, assuming a weight of close to 0.0 grams for the very small, undeveloped testes of birds collected in winter.

Second, as has been pointed out, the intestinal tracts of specimens taken in winter are longer than the intestinal tracts of specimens taken in the summer. The difference between the mean lengths of the gut in the two seasonal samples is about 4 mm. (fig. 2). The measurable intestinal tracts of three of four birds collected on February 13 and 14, 1960, were measured and weighed and an average figure was obtained of 0.1 grams per millimeter of the entire intestinal tract. On this basis, some 0.4 grams of the seasonal weight difference could be accounted for on the basis of the increase in the length of the gut in winter. Baldwin and Kendeigh (1938:434) suggested that "seasonal changes in weight may possibly be correlated also with changes . . . in length of digestive tract or other organs," and the present data bear out the validity of their suggestion.

Finally, as has been noted previously, there is a noticeable decrease in the amount of dirt and grit present in the stomach contents of summer-taken birds. The four birds collected in February, 1960, had considerable amounts of such material in their stom-

achs. The stomach contents of these birds averaged 0.9 grams and appeared to contain about 25 per cent inert material. Since dirt and grit undoubtedly weigh more per unit of volume than the seeds, chunks of acorn, and small insects which made up the remainder of the stomach contents, an estimate of 0.2 grams seasonal difference in the weight of the inert material in the stomach contents seems fairly conservative.

On the basis of testis growth, increase in gut length in winter, and seasonal variation in the amount of inert material present in the stomach contents, one can account for approximately 1.1 grams of the total difference between the highest mean weight, 45.04 grams for the combined samples taken in December and January, and the lowest mean weight, 38.10 grams for the sample taken in June. This is a total of 15.8 per cent of the total difference of 6.94 grams. One may hypothesize, since we are dealing with an essentially non-fat-depositing population, that the remainder of the difference is made up of the cumulative seasonal variation in weight of a number of organs and tissues. What is clearly needed is a detailed study of weight in a resident population which does not have a fat cycle, establishing seasonal variation in weight and attempting to correlate this with seasonal variation in the weight of the stomach contents and of as many organs and tissues as possible. Such a study would serve to explain, at least in part, just what is involved in seasonal variation in weight and it would also serve to demonstrate some of the adjustments made by the individual to seasonally changing environmental conditions.

SUMMARY

Significant seasonal variation is shown in bill length, length of the intestinal tract, and weight in a resident population of the Rufous-sided Towhee (*Pipilo erythrophthalmus megalonyx*).

The short bill and long intestinal tract of birds taken in winter apparently correlate with the vegetable diet utilized at that season; the long bill and short intestinal tract of birds taken in summer apparently correlate with increased consumption of insect material in the summer period.

Weight of adult males decreased sharply and nearly steadily during the breeding season, the decrease apparently correlated with the diversion of time and energy from foraging and resting to breeding season activities. Since the population under study did not have a well-marked fat cycle, seasonal variation in weight cannot be explained in terms of fat deposition and consumption. Part of the difference between the high and low points of the weight cycle could be accounted for on the basis of testis growth, increase in the length of the intestinal tract in winter, and seasonal variation in the amount of inert material present in the stomach contents.

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THE SELECTION OF COLORED NEST BOXES BY HOUSE WRENS

By Robert A. McCabe

This paper describes and evaluates a field experiment on the choice of colored nest boxes by House Wrens (*Troglodytes aedon*). The literature on the experimentation with color recognition and color discrimination among animals, and among birds in particular, is relatively large and spans a considerable time period. A brief summary is given by Smith (1945). A general review of past experimentation for comparison with my study left one outstanding impression, namely, that a review of color vision in birds is urgently needed. Such a review is not attempted here. The first part of this paper, however, will endeavor to sample the available works in order to point up the complexity of color appraisal. In only a few relevant cases was an effort made to cover the substantial, untranslated foreign literature.

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SOME COLOR RELATIONSHIPS AMONG BIRDS

Color differentiation by birds is said by Worden (1958?) to have been postulated by Thomas Young in 1807. Testing of color awareness was at first confined largely to laboratory research (Yerkes, 1915; Lashley, 1916; C. Hess, 1907; Bailey and Riley, 1931; Walls, 1942; and others). In general, it can be said that physiologically birds distinguish color, although the spectrum range is not clearly defined; that diurnal birds are stimulated more by red-yellow color bands and nocturnal birds by blue-green color bands; that birds generally react to color on the basis of wave length, that is, color tone; that the function of the oil droplets of the retina as color filters is not completely understood; and lastly, that there is some evidence to show that when the intensity of illumination is decreased, the darkening effect is greater on red, orange and yellow than on blue or green, so that the point of maximum brilliance in the spectrum under reduced illumination shifts from yellow into green (Purkinje effect).

Investigations into the function of color in the lives of birds can be divided into four general types: color associated with food, natal behavior, nesting activity, and egg recognition.

Color associated with food.—The field experiments with color are few, because as Lashley (1916) points out, it is virtually impossible to control outdoor illumination. This fact notwithstanding, some interesting findings have been made by field testing, and some inadvertent field situations have lent themselves to the appraisal of color discrimination among birds. As in laboratory experiments, the field tests for the most part showed association of color with food.

In the late 19th century, the destruction of yellow crocuses by sparrows in England was attributed to color choice, particularly since white and blue crocuses were spared (Shaw, 1876; Stokoe, 1877, and others). Tegetmeier (1877) immediately countered that he found all three kinds attacked by sparrows and that it was just a matter of learning since the yellow crocus was most common. W. White (1891) discussed briefly whether or not this attack on crocuses is antipathy for the color and concluded that it is "fondness" rather than antipathy that provoked the attack. So ends the case of the crocuses.

G. White (1877) also mentioned color awareness when he wrote that, "birds are

much influenced in their choice of food by colour, for though white currants are a much sweeter fruit than red, yet they seldom touch the former till they have devoured every bunch of the latter."

The large number of plants having red berries may be the result of birds being attracted to them because of the red color, thereby scattering the seeds more widely, according to G. Hess (1951). The propensity of some birds for the red color is also reported by Pickens and Garrison (1931). Ruby-throated Hummingbirds (*Archilochus colubris*) visited colored flowers in a garden where red comprised 4 per cent of the available flower color. In three separate trials, 41, 33, and 38 per cent of the visits were made to red flowers, in the series of 12 possible color selections.

Lyerly, Riess, and Ross (1950) used one female Mexican Violet-eared Hummingbird (*Colibri thalassinus*) and generous application of statistics in selection tests of feeding bottles colored with fingernail polish. They found that only yellow was chosen significantly fewer times than red, green, and blue. Among the latter colors there was no statistical difference.

Marples (1933) fed colored peanuts to wild tits (*Parus major* and *P. caeruleus*) and nuthatches (*Sitta europaea*). He alternated colored with uncolored offerings and also placed the peanuts in concentric rings in some tests so as to eliminate position bias. His experiments were well conceived but poorly executed and inadequately interpreted since in each of five trials he changed the number of available colors and there is no short summary of his results. If one takes some of his test colors, using only those employed in all five tests, and rates these on an arbitrary scale of five points for first choice, four for second, and so on, the natural uncolored nut ranked first, the white nut second, the orange third, the green fourth, and the dark blue fifth. Red and purple were a poor tie for sixth position (table 1).

TABLE 1

COLORED PEANUTS FED TO CERTAIN BIRDS[1]

Color	Test number[2] 1	2	3	4	5	Points	Average
Orange	1(5)	2(4)	5(1)	7(–)	10(–)	10	2.0
White	5(1)	1(5)	1(5)	6(–)	2(4)	15	3.0
Green	2(4)	3(3)	6(–)	10(–)	7(–)	7	1.4
Dark blue[3]	7(–)	5(1)	4(2)	3(3)	12(–)	6	1.2
Purple	4(2)	9(–)	7(–)	6(–)	4(2)	4	0.8
Natural	3(3)	4(2)	2(4)	1(5)	1(5)	19	3.8
Red	6(–)	10(–)	9(–)	2(4)	9(–)	4	0.8

[1] Adapted from Marples (1933).
[2] Numbers outside of parentheses indicate order in which bird involved in test chose nut; numbers inside parentheses are points given for choice. Five points were given for first choice, 4 for second choice, and so on.
[3] Called Prussian blue in tests 3, 4, and 5.

Kalmbach (1943) also found that natural grains ranked ahead of artificially colored grains fed to a variety of birds under pen conditions. In summarizing, Kalmbach states, "On the basis of work done with English Sparrows [*Passer domesticus*] and House Finches [*Carpodacus mexicanus*], supported less emphatically by observations on pheasants, chickens, pigeons and waterfowl, most pronounced aversion manifests itself with respect to foods dyed with colors near the center of the humanly visible spectrum, in the yellow and green sectors." Although color can be evaluated accurately in each test situation, there appears to be no common pattern discernible in all tests or exact duplication in any two.

Psychological test associations with color.—A recent paper by E. Hess (1956)

supports Kalmbach's findings in part. Hess examined the preferences of chicks and ducklings for objects of different colors in the laboratory. The results from his experiments with young domestic chickens supported Kalmbach's conclusions. Hess states, "For the chicks there is a bimodal preference to color, with one peak occurring in the orange region of the spectrum and a second peak in the blue region." Hess' ducklings and Kalmbach's Bobwhite (*Colinus virginianus*), however, presented opposite effects for the respective experiments. The relationship of bird behavior to color is seldom, if ever, without an aberrant situation. Schaefer and Hess (1959) attempted to imprint newly hatched domestic chickens with certain pure colors rated on the Ostwald color system. This laboratory experiment is somewhat involved and the details are not pertinent here. The results rate the following colors from best to poorest as imprinters: blue, red, green, orange, gray, black, yellow and white. A concluding remark indicates that the writers also found an inverse relationship between imprinting and "pecking for food objects of the same coloring."

Nesting conditions associated with color.—The aversion of Baltimore Orioles (*Icterus galbula*) to red strings in nest building (M. Smith, 1928) and the use of blue material to the exclusion of red and yellow by the Satin Bower Bird, *Ptilonorhynchus violaceus* (Edwards, 1920) are further observations on apparent color choice by birds in the wild.

A very interesting experiment in color awareness was conducted by S. Smith (1945) who constructed plastic fecal sacs which were placed on the rims of nests containing young birds. The natural inclination of the adults to keep the nest clean caused them to remove the false fecal sacs. In one set of five trials involving a pair of Meadow Pipits (*Anthus pratensis*), green, white, yellow, red and purple fecal sacs were removed in that order. In two of these trials the purple sac was ignored. Four similar trials at the nest of a Yellow Wagtail (*Motacilla flava*) showed the order of removal by the male to be yellow, purple, white, green and red. In the latter case the female removed only white artificial sacs. Smith (*op. cit.*) makes no sweeping claims for the data but states that there "may be a correlation between the colour awareness of a bird and the plumage colours of the species. . . ." I saw no such relationship in this or other color-awareness situations. Edwards (*op. cit.*) reported that the Satin Bower Bird which appeared to prefer blue objects with which it adorned its nest also had blue eyes.

Eggs and color associations.—McClure (*in* Kalmbach, 1943) states that in Mourning Doves (*Zenaidura macroura*), whose eggs are white, one "can color them any color you can conceive of" and the bird will continue, with only slight hesitation, to incubate the colored eggs. Not all birds are so undiscerning. Tinbergen (1953) in his field experiments with Herring Gulls (*Larus argentatus*) on egg recognition substituted colored eggs for the normal eggs in a series of nests. His conclusions were "that various colours have about equal releasing value, although there are indications that the natural colours are somewhat more stimulating than blue and yellow. Red, however, is definitely less stimulating, and even releases another response." Herring Gulls also refused to accept red eggs in the experiments of Goethe (1937).

The crux of the information discussed here is that there is no clear-cut pattern of reaction to color by various groups of birds or by birds in general. Each test seems to be conditioned not only by color but by attendant circumstances. Indeed the experimental situation may be the essential factor determining the color selected or rejected.

HOUSE WRENS AND COLORED NEST BOXES

My experiment was conducted to test whether House Wrens would discriminate among identically constructed nest boxes that were painted different colors. The type

Fig. 1. The five-can battery of colored nest boxes of House Wrens (*Troglodytes aedon*). Note the single top and ready access to box contents.

of nest box used in this experiment was a number 10 (2-quart) tin can with a removable wooden top and a circular entrance 2 inches in diameter. Some of these boxes were attached singly to fence posts for a general study of wrens and others were fixed together as a battery of five cans of assorted colors (fig. 1) with a single wooden top.

The male House Wren builds the major portion of the nest including the nest cavity. It remains only for the female to add the nest lining of fine materials before the eggs are laid. The male also carries nesting material to other likely sites nearby. The amount of nesting materials deposited in each box was used as an indicator of the preference for each box.

The tendency of wrens to be intolerant of other wrens nesting close by allowed for only one pair to occupy a single box in the battery of five boxes lined up side by side. Five colors were used: red, green, yellow, blue, and white. The Munsell (1942) ratings are as follows:

Hue (color)	Red	Yellow	Green	Blue
Value (brightness)	4	8	4	4
Chroma (saturation)	+10	8	6	8

These colors faded, often differentially, between years, and the batteries of nest boxes were repainted when the colors faded sufficiently to be detected by my eye. The position of any one color was rotated so that in five batteries every color occupied a different position in each battery. In any one year, 5, 10, or 15 batteries were placed in the field. Unfortunately not all the batteries were occupied by wrens in every year.

The results of 11 years' testing are shown in table 2. There was no statistically significant difference in choice among the various positions in the battery irrespective of color. Of the 98 boxes containing complete nests, red and green were obviously selected in preference over the remaining three colors. In order to test the statistical significance, if any, among the five colors, the Duncan multiple range test was applied (Duncan, 1955). This test compares each color with every other color. The results are presented in table 3. There was no difference between red and green, green and blue, blue and yellow, yellow and white. The differences among other combinations were

TABLE 2

COLORS AND POSITIONS SELECTED BY HOUSE WRENS IN NESTING BOX BATTERIES

Position	Red	Green	Yellow	Blue	White	Total
I	11	9	1	2	0	23
II	5	7	0	1	0	13
III	5	2	0	3	0	10
IV	7	6	1	7	2	23
V	13	7	6	3	0	29
Total	41	31	8	16	2	98

significant at levels ranging from .01 to .05. Since there was no difference between red and green, I suspected that old wrens that had nested in one of our many single green boxes in previous years might have returned and again used a green or a red box in the test battery. This happened in only one case, and the banded wren that had previously used a green box returned to nest in a blue box.

Table 3 deals with boxes in which a complete nest was made and at least one egg deposited. In a battery containing such a nest, other boxes also contained nesting material in varying amounts. The same holds for batteries where only a male nest was present and the other boxes had lesser amounts of nest material. In cases where the amount of nesting material could be rated on the basis of 5 points for the most, grading to 1 point for the least amount, 44 batteries were rated. As for the batteries containing complete nests, red and green were again preferred and showed no statistical difference at the .05 level in the preference (amount of use) between them by the wrens. The same was true among white, blue, and yellow, but these latter colors were preferred statistically less (.05) than red and green.

TABLE 3

STATISTICALLY SIGNIFICANT DIFFERENCES BETWEEN PAIRS OF COLORS OF NEST BOXES OF HOUSE WRENS

	Red	Green	Blue	Yellow	White
Red	....	0	.05	.01	.01
Green	0	....	0	.01	.01
Blue	.05	0	....	0	.05
Yellow	.01	.01	0	....	0
White	.01	.01	.05	0	....

One breakdown in the tolerance of the House Wren and also of the Tree Swallow (*Iridoprocne bicolor*) occurred in the nesting season of 1954 when a pair of each species nested in one of the batteries of colored boxes. The wren began nest building first and was followed in about three days by the Tree Swallow. The first egg was laid by the wren. On the following day the Tree Swallow laid the first egg of a clutch of four. The wren continued its laying until a clutch of six had been laid. Both females incubated, and all eggs hatched. The young of both species were fed without interspecific strife for six days when both nests were destroyed by a raccoon. I am confident that both sets of young would have fledged, as the birds had become spacially adjusted to each other. The Tree Swallow used the yellow box in position one and the wren used the red box in position five. In this case position was perhaps more important than the color of the box to the Tree Swallow because it nested after the wren had begun nesting. The distance between the entrances of the two end boxes was about 26 inches.

Wrens are usually double-brooded and frequently nest a second time in the same area if a site is available. Second nests of battery-using birds were sometimes placed

TABLE 4

COMPARISON OF COLOR OF ORIGINAL NEST BOX WITH THAT OF SECOND NEST BOX

Original nest	Second nest: Red	Yellow	Green	Blue	White
Red	8	....	1	....	....
Yellow	....	1	....	....	....
Green	2	....	3	....	....
Blue	1	....	1	2	....
White	....	....	....	....	1

in the same battery. When this occurred, there was a tendency to nest in the same box that had been used for the first nest. The boxes were cleaned by us as soon as the young fledged, but often renovation by the wren occurred in a day or two after fledging. The new nest was often only a thin layer of nest material over the first nest, if it had not been removed, plus a new nest lining. Of 20 known second nestings, 15 were in the same box as that used for the first nest (table 4).

In three cases, a pair of wrens nested simultaneously in two boxes. In all of these nestings, white was one of the "colors" involved (table 5). Since there was no difference between various pairs of colors (for example, red-green, green-blue, blue-yellow, and so on), the double nesting conceivably might have been one of color confusion. This, however, was not the case; instead it appeared to be a matter of position in the battery. In all instances, the two boxes were adjacent to each other, but the exact position was not recorded for one combination. Only one nest was successful in fledging its young, although young were hatched from one box in each of three pairs of boxes. The failures were not associated with the compound nesting effort.

TABLE 5

SIMULTANEOUS NESTING OF HOUSE WRENS IN BATTERIES OF COLORED NEST BOXES

	1944	1947	1951
Color	R–W	R–W	B–W
Position	5–4	4–3	?–?
Eggs	4–4	4–3	1–4
Young	4–0	3–0	0–2

The nesting success of 57 per cent for the general study where 336 single boxes were used is barely different statistically (chi-square test) from the 66 per cent recorded for the 98 colored boxes in the batteries. This can be accounted for, I believe, by reason of the fact that the color-test boxes were usually placed in the best possible sites in order to insure acceptability. This no doubt improved the chances for successful nesting as well.

DISCUSSION

This study adds another piece to a multi-unit mosaic on the role of color in the life of a bird. No attempt has been made here or elsewhere to put the pieces in order. There is no readily discernible pattern on the acceptance or rejection of given colors by birds, and often contradictory data present themselves. This apparent lack of conformity may lie in the difficulty of removing attendant variables associated with the testing situations. The relationship of brightness to color saturation is not always available for comparison in the various experiments nor are the colors always measured by the several color standards. Conditions in the wild are particularly difficult to control, yet it is here that the ecologist particularly wishes to resolve his problems.

The basic biology of color has wide interest and application. There is doubtless considerable evolutionary significance in the choice of color or association with color among birds and mammals and invertebrates as well. Yet this aspect of natural history is relatively unexplored. A knowledge of color preference or aversion could be used in animal control and management, particularly in control of pests by use of lethal baits or in discouraging nuisance activity or depredation by wild or feral animals. When the physiology, biochemistry, neurology, and ethology of the relationship of color to birds has been worked out, the widely scattered information now in the literature will add materially to the expanding picture of color biology.

SUMMARY

For 11 years, House Wrens (*Troglodytes aedon*) were given a choice of red, yellow, blue, white, and green nesting boxes. Each colored box was rotated in batteries of five boxes each. Of 98 nests constructed in the boxes, red and green were preferred and white was used least. There was no significant difference in the position of the accepted boxes in the battery. Wrens nesting for the second time within the year in a battery tended to use the same box occupied by the first nest. Three simultaneous nesting efforts within a battery were influenced by position rather than color, as the two nests were in each case adjacent to each other. A general study of wrens using single green boxes showed a 57 per cent fledging success, compared to 66 per cent in the colored batteries. This can be accounted for on the basis of better sites being used for the batteries.

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SOCIAL STIMULATION WITHIN BLACKBIRD COLONIES

By Gordon H. Orians

In 1938, F. F. Darling, writing about breeding colonies of gulls, suggested that (p. 3) "The social group and its magnitude, in birds which are gregarious at the breeding season, are themselves exteroceptive factors in the development and synchronization of reproductive condition in the members of individual pairs of birds and throughout the flock."

Support for this hypothesis was drawn from three types of evidence: the time of initiation of breeding; the synchrony of colony members; and the comparative breeding success of large and small colonies. On the basis of his results, Darling also postulated a number of corollaries, but it is important to note that the validity of the main thesis does not rest upon the truth of these corollaries. First, he suggested that synchrony was of value in reducing the loss of young to predators because the vulnerable stages were concentrated into a shorter period of time. Second, he believed that there was a threshold of numbers below which breeding would be unsuccessful. He did recognize, however, that this number may change with ecological conditions. Finally, he postulated that sexual dimorphism and elaborate displays had evolved because they stimulated the pituitary glands of other members of the breeding group. This explanation was thought to avoid some of the traditional difficulties felt in the Darwinian theory of sexual selection.

More recently, Darling (1952) extended his main thesis to cover territorial birds as well, postulating that the main value of a territory was that it provided a periphery of contact between pairs, thus offering greater opportunities for social stimulation. According to this view the area is defended primarily because the act of defense provides the stimulation necessary to bring the birds into reproductive condition and not because the area provides any vital requisites. The concentration of territories of breeding birds into pockets in what appears to be a uniform environment was offered as suggestive evidence in support of the hypothesis.

Early it was brought out that some of the supposed differences in success observed by Darling could be explained by variable age distributions (Lack, 1943; Armstrong, 1947), and it was subsequently demonstrated that Darling's original data were statistically insignificant (Haartman, 1945). Nonetheless, belief in the effectiveness of the "Darling Effect" became widespread (Lockley, 1942; Lowe, 1954) and it was even suggested that interspecific stimulation was important in mixed breeding colonies (Fisher and Lockley, 1954). However, neither the original ideas of Darling nor the suggestion of Lack and Armstrong were subjected to critical investigation until recently (Coulson and White, 1956, 1958, 1960).

Extensive data gathered on the ecology of social organization in Redwinged (*Agelaius phoeniceus*) and Tricolored (*A. tricolor*) blackbirds in north-central California (Orians, in press) afford the opportunity to examine timing, synchrony and breeding success in relation to colony size in these two species. The Redwing is not colonial in the strict sense of the word, but the size of territories is small and the males engage in conspicuous perched and aerial displays above the vegetation so that opportunities for social stimulation are good. The Tricolored Blackbird, on the other hand, is the most highly colonial of North American passerines (Neff, 1937; Lack and Emlen, 1939), and up to 100,000 nests may be concentrated in a few acres of marsh. Here, conditions for social stimulation should be maximal.

THE REDWINGED BLACKBIRD

In the Redwing, the time at which territories are first occupied and the amount of time spent on them early in the season vary greatly from place to place, but this is not correlated with colony size. Since all suitable habitat is fully occupied, the size of the breeding population is determined primarily by the size of the marsh and secondarily by the nature of the surrounding vegetation. Where extensive feeding areas immediately surround the emergent vegetation in which the nests are placed, most of the food is gathered off the territories and territories are the smallest (Orians, in press). Peripheral territories that are most advantageously located with respect to feeding grounds are most fiercely contested and are occupied first during the breeding season. The time of arrival of females and the onset of nest building parallels the pattern of territory establishment by the males, and territory contests among females are also most severe for peripheral areas. Therefore, breeding may on the average be later in larger marshes simply because there is less periphery per unit of nesting area. In California, where the breeding period comes at the end of the rainy season, the peak populations of insects are present earlier on the grasslands, which dry up in May or June, than on the marshes. Since peripherally located birds feed more away from the marsh than birds with territories in the interior of the marsh, it is reasonable to assume that this difference in timing is adapted to coincide with the maximum availability of food and not with any effects of social stimulation. No significant differences in time of breeding in Redwing colonies of different sizes were found by Mayr (1941) or Smith (1943).

Synchrony in this species is poor because of polygamy and the tendency of the several females of each male to be out of phase with each other. Renestings and second broods further complicate the picture. However, data are available on the dates at which first nests were started in seven small, isolated cattail patches at the East Park Reservoir, Colusa County, California, in 1960. Even when data for all seven areas are lumped together, 51 of 72 first nests were started within three days, the closest synchrony I have observed in this species. The spread of time during which first nests were started in the main marsh on the reservoir extended over a much longer period of time because nesting in central territories started later than in peripheral territories as already indicated. It is probably generally true in this species that the spread of breeding is greater in larger colonies (Smith, *op. cit.*).

Insufficient data are available to compare nesting success in colonies of different size. The nesting area at Jewel Lake, near Berkeley, California, was surrounded by oak forest with the result that the chief source of mortality was predation by the Scrub Jay (*Aphelocoma coerulescens*). In the dry foothills of Colusa County, on the other hand, starvation was the major cause of mortality. For any meaningful analysis of the influence of colony size on breeding success, colonies of varying size in comparable environmental situations would have to be studied, and such studies are not available. No differences in reproductive success correlated with colony size were discovered in Illinois by Smith (*op. cit.*).

THE TRICOLORED BLACKBIRD

Data on the date at which nest building started are available for 25 colonies of the Tricolored Blackbird ranging in size from 50 to about 100,000 nests (table 1). On the average, the larger colonies started later but this difference is related to the ecology of the breeding area rather than colony size *per se*. The breeding habitats of this species in California can be grouped into three main categories: the foothills, valley cropland with no rice, and the rice-growing country. Breeding begins first in the foothills and last in the rice-growing country (table 2). In the foothills, where there is little or no irriga-

tion, the insect supply doubtless diminishes sharply when the grasses dry up in May or early June. In the valley, where much of the land is irrigated, the country remains productive of insects for a much longer period. Moreover, the rice fields are not seeded until late April or early May, and until the grass has sprouted and the water level in the fields lowered three weeks later, there are neither feeding grounds nor food supplies

TABLE 1

TIME OF BREEDING IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Colony size	Number of colonies	Mean starting date	Range of starting dates
Less than 1000 nests	7	May 2	Apr. 21–May 17
1000–10,000 nests	5	Apr. 28	Apr. 15–May 17
More than 10,000 nests	13	May 9	Apr. 1–May 28

for the birds. It is not until the vigorous growth of the crop in the warm shallow water is fully under way in June that the maximum feeding potential of the area is realized. Since the rice country provides the best conditions for the breeding of the Tricolor and supports the largest colonies, the larger colonies tend to start later, and no influence of social stimulation can be detected.

Colonies of Tricolored Blackbirds of all sizes are characterized by remarkable synchrony of nesting. Normally, all nests are completed within a period of one week, but sometimes colonies grow peripherally and, rarely, new nests may be constructed throughout the colony (Orians, 1960). In colonies studied by me, the largest had the longest duration of egg laying. But if those colonies growing peripherally are excluded, synchrony is comparable in all size classes (table 3). There is thus no evidence of a stimulating effect of numbers upon synchrony.

If numbers are important in stimulating the reproductive cycles of colony members it might be expected that clutch sizes would, on the average, be larger in large colonies

TABLE 2

TIME OF BREEDING IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO HABITAT

Habitat	Number of colonies	Mean starting date	Range of starting dates
Foothills	8	Apr. 23	Apr. 1–May 17
Valley cropland (no rice)	6	May 2	Apr. 18–May 23
Rice country	11	May 15	May 1–May 28

than in small colonies. However, the results of determinations of clutch size in seven colonies (table 4) show no signs of the effects of social stimulation.

Nesting success in colonial species is notoriously difficult to determine. In the Tricolor desertions sometimes occur, probably in response to unfavorable feeding conditions in the surrounding environment (Orians, 1960). Moreover, the chance of loss to predators probably depends not only on colony size but also on the location of the colony with respect to habitat suitable for different predators and the accessibility of the nests. The effects of colony size *per se* in increasing the nesting success could only be determined if sufficient colonies of all sizes were available for a wide variety of environmental situations. As yet no such data are available nor are they likely to be obtained easily because, since colony size varies with environmental conditions, it is difficult, if not impossible, to find colonies of all sizes in all situations. Nonetheless, I have been able to determine the average size of colonies which failed completely (table 5). Complete failure has been more common in smaller colonies but in only some of these instances

could it be attributed to predators. In some cases desertion due to drought is indicated and usually it is the smaller colonies that are located in marginal situations where the effects of adverse weather are most strongly felt. Thus, nesting success does not appear to be very useful in evaluating the possible effects of social stimulation upon the breeding colonies.

TABLE 3

BREEDING SYNCHRONY IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Colony size	Number of colonies	Mean duration of egg laying	Range
Less than 1000 nests	6	7.5 days	5–18 days
1000–10,000 nests	5	6.2	4–10
More than 10,000 nests	13	19.1	5–41
(Excluding concentrically growing colonies)	(7)	(7.1 days)	(5–10 days)

The three types of evidence which Darling sought in support of his thesis provide no support for the operation of social stimulation in colonies of Tricolored Blackbirds. It might be argued that all colonies of this species which I investigated were large enough to provide maximal stimulation to their constituents, but such an answer automatically relegates social stimulation to a position of minor significance. However, although it has been shown that time of breeding is not correlated with colony size but rather is related to feeding conditions in different habitats, certain features of timing remain unexplained. Outside the breeding period Tricolored Blackbirds are highly nomadic and are found largely within the Great Valley of California. Often flocks appear suddenly in areas from which they have been absent for months and immediately breed. Frequently, colonies in close proximity to each other may be strongly out of phase with each other. For example, three colonies in the rice fields north of Sacramento started on May 1,

TABLE 4

CLUTCH SIZE IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Colony size	Number of colonies	Total number of clutches counted	Mean clutch size	Range of mean clutch sizes
Less than 1000 nests	3	425	3.40	3.29–3.44
1000–10,000 nests	2	311	3.11	3.01–3.33
More than 10,000 nests	2	1433	3.09	3.09–3.11

May 8, and May 15, 1959, in spite of their being in uniform country and within two miles of each other. Unfortunately, I was not present when these particular birds appeared and so I could not determine whether or not they arrived in three separate, already integrated flocks. Although the possibility of subtle environmental differences between these sites, such as differences in the time of planting of the rice, cannot be ruled out, it is likely that there is considerable social stimulation within these nomadic flocks which results in their spectacularly synchronous breeding because the birds are probably in an advanced state of gonadal preparation while still wandering about. Social stimulation would be highly advantageous for a nomadic, colonial species adapted for utilizing ecological opportunities whenever and wherever they occur, because it would enable the wandering flocks to be able to respond immediately and simultaneously to favorable situations whose duration may be short as well as temporally and spatially unpredictable. It is important to note, however, that such social stimulation, if subsequently shown to be true, is not related to the territorial and mating displays which are used once breeding begins and which were the basis for Darling's original postulation.

DISCUSSION

In view of the difficulty in obtaining convincing evidence of the "Darling Effect" in spite of repeated efforts, and because of the widespread uncritical acceptance of the theory despite the lack of supporting evidence, it is desirable to consider whether the failure to obtain evidence lies with the hypothesis in general or with the sorts of evidence sought or both.

Theoretically, the hypothesis of social stimulation is certainly plausible, a fact which probably is responsible for no small part of its acceptance. Moreover, it is known that the maturation of female reproductive tracts lags behind that of the males in many

TABLE 5

NESTING SUCCESS IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Degree of success	Mean colony size	Range
Complete failure	2080 nests	600–6000 nests
At least partial success	36,570	50–100,000

species and that the females come into breeding condition only when they reach suitable breeding grounds where the males are already displaying. The evolution of this response is perhaps best explained in terms of the selective consequences of the relative energy expenditures of maturing and maintaining testes and ovaries (Orians, in press). In any case, there appear to be no good theoretical grounds for rejecting the operation of some form of social stimulation among birds even if one wished to reject its use to explain the evolution of coloniality or territoriality.

However, more serious objections may be raised to the three types of evidence which Darling sought in support of his hypothesis, because important ecological variables were ignored. For example, it is necessary to assume that the modal breeding period of any species is the most advantageous time at which to breed. In species raising more than one brood, timing problems are more complex but the general principle holds. If this were not true the time of the breeding period would be shifting in one direction or the other under the influence of natural selection. This immediately raises the problem of the supposed selective advantage of earlier breeding in the larger colonies. Apparently neither Darling nor Coulson and White (1960) attached particular selective significance to these differences, but any feature of reproductive biology is likely to be under strong selective pressure and we must conclude that any tendency toward earlier breeding which might be fostered by social stimulation must necessarily be opposed by the action of natural selection. Moreover, differences in timing are already apparent at the time the birds arrive on the breeding grounds so that it is necessary to postulate that the effects of social stimulation carry over from one season to the next but this is highly unlikely. In any case, this makes social stimulation into quite a different phenomenon than originally constituted.

It was early pointed out by Lack (1943) and Armstrong (1947) that age composition of colonies of such birds as gulls and fulmars had been ignored by Darling and others subsequently applying his ideas. Since older individuals are known to breed earlier than younger ones and since many small colonies are composed of young birds, differences observed among colonies might be due to this cause. Apparently this suggestion was without effect until Coulson and White (1956, 1958, 1960) carefully investigated the age structure of colonies of the Kittiwake (*Rissa tridactyla*) and the influence of age on time of breeding. Through intensive studies of marked individuals they determined that birds bred progressively earlier in subsequent years and that the small colonies they

investigated contained a higher percentage of younger birds. Nonetheless, differences in time of breeding which could be attributed to age composition could account for only part of the differences observed. Apparently no selective advantage for earlier breeding by older individuals has been suggested, but it may be that because of their greater efficiency in food gathering older birds are able to do better earlier when the total food supply is less. Alternately, the advantage may be related to the obtaining of the best nesting sites.

Darling assumed that synchrony was necessarily good, and it is true that short duration of food supply, the advantages of communal exploitation, or the action of predators may favor synchrony, but there are good ecological reasons for believing that asynchrony may be more advantageous under many circumstances. If the food resources exploited by the breeding population are available for relatively long periods of time and, moreover, if there is recruitment to the food supply during that period, it may be decidedly advantageous to a population to spread its breeding effort rather than to concentrate it. Thus, lack of synchrony cannot be interpreted as detrimental to any species unless a careful ecological study has revealed this to be so.

Comparative data on breeding success are even more difficult to obtain and interpret. It is well known that in most species breeding occurs in suboptimal as well as optimal habitats. In territorial species the territories are smallest in the latter and in colonial species the colonies are largest. This was clearly demonstrated in the case of the Tricolored Blackbird, and other instances are discussed by Lack (1954). There is also evidence that breeding is less successful in suboptimal habitat than in optimal although it is not known how widespread this is (Kluijver, 1951; Lack, 1958; Orians, in press). Thus it is to be expected that small colonies of birds would have poorer breeding success than larger colonies, social stimulation or not. In Darling's analysis of breeding success, and in all subsequent analyses as well, the size and density of breeding colonies are the only variables which have been considered. Investigators have readily assumed that the environment is uniformly suitable for all breeding localities under consideration. Whereas it may be relatively easy for a terrestrial human to ignore spatial and temporal variations in the oceanic environment which are of significance to birds, it is difficult to ignore them in terrestrial conditions. Nonetheless, this has been done in previous studies of the Redwing (Mayr, 1941; Smith, 1943) although Smith clearly recognized the presence of spatial variability. Coulson and White also assumed ecological uniformity of environment for colonies of Kittiwakes. This assumption may be all the more hazardous in colonial species in which, because of the large numbers of individuals utilizing the environment from a single spot, the distance an individual must fly to procure food for the young and the searching time for, as well as the energy content of, individual food items become of paramount importance. These may be strongly influenced by the number of birds involved and the precise location of colonies with respect to suitable feeding areas that doubtless vary both spatially and temporally. Therefore, it may be strongly doubted whether pursuit of the three types of evidence originally suggested by Darling will prove very fruitful in determining the role of social stimulation in avian social organization.

Darling originally thought that there would prove to be a lower limit to colony size below which successful breeding was impossible. It has since been repeatedly shown that isolated pairs of normally colonial birds are physiologically quite capable of successful reproduction. The extension of the hypothesis to territorial species demands more careful attention however. It was first suggested by the clumping of territories in apparently uniform habitat. We may consider the possibility of both accepting and rejecting the assumption of uniformity of the habitat. It is obvious that caution is always necessary because what appears uniform to the human observer may not be uniform to the bird

in question. However, it is possible to press this argument too far inasmuch as no two places are ever identical and thus the critic can always find subtle differences to which he can point. To determine whether these differences are really responsible for the clumping is no easy matter.

Alternately we may accept the postulate of environmental uniformity in these cases and ask whether clumping might nevertheless result irrespective of any stimulatory effect of displays upon reproductive physiology. The most likely possibility is that one of the cues which a bird uses to evaluate the suitability of a habitat is the presence of other birds of the same species. Such a response should be advantageous because presumably earlier arrivals would have departed had the area not been suitable. It is this attraction of newly arriving birds to individuals already present which forms the basis for the use of decoys in duck hunting, probably a special case of a widespread phenomenon. Thus, clumping might be produced in this manner in the absence of any need for social stimulation in the narrower sense in which Darling employed the term.

It might be argued that since continued efforts have failed to produce good evidence of the Darling Effect and since the interpretation of data is fraught with difficulties, that the effect is nonexistent, or, if existent, not demonstrable, but neither conclusion necessarily follows.

In spite of the ecological difficulties inherent in any investigation of social stimulation, modified techniques may prove to be useful. Data from the Tricolored Blackbird suggest that in nomadic species where the flock may be very close-knit prior to the initiation of breeding, and where the selective value of rapid and synchronous response to suitable conditions is great, social stimulation is likely to play an important role, even though this role is somewhat modified from the sort of stimulation envisioned by Darling. Nomadic species are unable to use the standard environmental clues, such as daylength, in the same manner as species with predictable breeding periods in more stable environments (Marshall, 1959). As yet, however, the gonadal cycles of nomadic species are largely unknown and even less is known of the responses of their reproductive systems to various environmental factors. Information currently being gathered in Australia indicates that nomadic species may remain for long periods with gonads in relatively advanced states waiting for suitable environmental conditions. When rain falls, breeding may be dramatically sudden (Allen Keast, personal communication) and the role of mutual stimulation may be important. Whatever the outcome of these investigations, nomadic species would seem to be better suited to studies of the significance of the Darling Effect than stationary colonial or territorial species where ecological variability appears to exert the dominant influence upon differences in timing, synchrony and nesting success. The evolution of territorial and colonial forms of social organization is strongly influenced by the ecology of environmental exploitation by the populations (Orians and Pitelka, MS), and any stimulation which appears is probably a minor secondary phenomenon in such species.

SUMMARY

Data from breeding colonies of Redwinged and Tricolored blackbirds in California were analyzed to determine the role of social stimulation in time of breeding, synchrony, and reproductive success. Variations in timing and synchrony in the Redwing were correlated with the nature of the marsh and its surrounding vegetation and not with size of the breeding population. In the Tricolored Blackbird time of breeding, synchrony, and clutch size were also found to be independent of colony size. Nesting success in both species could not be evaluated with respect to colony size *per se*.

Nonetheless, although most variability appears to be ecologically rather than socially

induced, there remain differences in time of breeding in colonies of Tricolors in close proximity to each other not obviously explained in this manner. Since flocks appear suddenly and breed immediately in areas from which they have been absent for months, group stimulation may operate in the nomadic flocks prior to the initiation of breeding.

The social stimulation theory currently fails to consider the selective significance of proposed changes in timing and synchrony and neglects important aspects of the ecology of the environment which may vary temporally and spatially. When these are taken into account the usual information sought in support of social stimulation is seen to be of limited use. Nomadic, colonial species are suggested as the best subjects for future studies of the "Darling Effect."

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FROM FIELD AND STUDY

Salivary Glands in the Black Swift.—In 1956 Lack (Auk, 73, 1956: 2) stated that all swifts use saliva in their nest building and that "all, so far as known, have enlarged salivary glands in both sexes in the breeding season." These general statements were questioned, however, by Johnston (Condor, 60, 1958:79) especially with regard to the Black Swift (*Cypseloides niger*). This species has been reported by Bent (U. S. Nat. Mus. Bull. 176, 1940:256–260) and Legg (Condor, 58, 1956: 183) to nest in situations where saliva would be unnecessary for construction of the nest; in fact, both men stated that saliva was not used in the nest. These reports do not preclude the possibility that Black Swifts do have salivary glands but just do not use them in nest building as do some other swifts.

An opportunity to resolve these apparently conflicting statements presented itself when I came into possession of two specimens of Black Swifts preserved in alcohol. The adult birds, a male and female, were taken at random from a flock at Vancouver, British Columbia, on June 13, 1960, by Dr. Miklos D. F. Udvardy. At this time the birds should have been nesting; the male had testes 9 mm. in length and the female had follicles 1.5 mm. in diameter. Gross examination of the floor of each bird's mouth did not reveal the presence of salivary glands which are so conspicuous in *Chaetura* and *Collocalia* (Johnston, Condor, 60, 1958:80; Marshall and Folley, Proc. Zool. Soc. Lond., 126, 1956:385), so histological sections of the floor of the mouth were prepared. After staining with hemotoxylin and eosin, these sections showed a few small lobes of the sublingual salivary glands, but each of these lobes was only 400 μ or less in diameter whereas those of the Chimney Swift (*Chaetura pelagica*) were shown by me earlier to be as much as 1000 μ.

From these data it is evident that the Black Swift does have sublingual salivary glands but that these glands are smaller than those found in some other swifts. These observations support the contention by Bent and Legg that saliva is not used in nest construction of this species.—David W. Johnston, *Department of Biology, Wake Forest College, Winston-Salem, North Carolina, January 5, 1961.*

Second Specimen of the Dovekie from Alaska.—An unsexed specimen of an adult Dovekie (*Plautus alle*) was received in 1948 from the late Roger Menadelook who collected it on Little Diomede Island, Alaska, July 8, 1948. It is now no. 9089 in my collection. Mr. Menadelook writes (*in litt.*) that this type of auklet "is very rare on this island, the occurrence being in my estimation about one in 50,000 of other auklets. The Eskimo name is Koogigahkrook. Weight 8 oz., wing spread 18 in., beak to tail tip 9½ in. Its wing beat is steady and unwavering like that of murres and its flight steady. The ones rarely seen here are all of the same color . . . but there is no knowledge of any laying eggs."

Gabrielson and Lincoln (The Birds of Alaska, 1959:483) report that "the only definite Alaskan record of this eastern Arctic species is a bird . . . [taken] . . . offshore at Point Barrow on July 13, 1935. This specimen, a high plumaged, unsexed adult, was sent to the Chicago Academy of Science where it is now No. 7864. . . . " The bird in my collection is the second known specimen from Alaska. —Wilson C. Hanna, *Colton, California, January 11, 1961.*

Growth Rate of the Lens of the Eye of House Sparrows.—The dry weight of the lens of the eye has successfully been used by Lord in aging cottontail rabbits, *Sylvilagus floridanus*, and gray foxes, *Urocyon cineroargenteus* (Jour. Wildlife Manag. 23, 1959:358–360; Jour. Mammal., in press). By weighing lenses of caged rabbits ranging in age from one day to 30 months, he found that the lens continues to grow in weight throughout adult life. Overlap in lens weights between one-year-old and two-year-old rabbits was slight. Because of this success with the lens technique in aging mammals, it appeared desirable to determine the growth rate for the lens of a bird in order to find out whether or not the same technique might also be useful in aging birds.

The more important characters that have been used to age birds are the degree of ossification of the skull in song birds, the presence or absence of the bursa of Fabricius, and the plumage in species with age-specific plumage characters (see for example, Miller, Bird-Banding, 17, 1946:33–35; Gower, Trans. Fourth N. Amer. Wildlife Conf., 1939:426–430; Selander and Giller, Condor, 62, 1960:202–214). These methods generally are limited to distinguishing first-year birds from older

birds. In only a few species of birds can second-year, third-year, and fourth-year individuals be distinguished from each other. For example, these age groups can be told apart in California Gulls (*Larus californicus*) by the plumage and by the color of legs, bill, eyelids, and gape (Johnston, Condor, 58, 1956:113–162, 206–221). The number of atretic and post-ovulatory follicles and the length of claws have been used as characters of relative age in Fulmars, *Fulmarus glacialis* (Wynne-Edwards, Proc. Zool. Soc. London, 109, 1939:127–132). However, no comparable structures are known for determining the age in years of most birds once the adult plumage has been attained.

House Sparrows (*Passer domesticus*) were collected by shooting, trapping, and raiding night roosts from February to October, 1960. Birds were taken in southeastern Michigan in the Ann Arbor area, in northern Michigan in Cheboygan County, and in California in Alameda County. There is no significant difference in wing length, bill length, bill depth, or tarsal length between House Sparrows from the eastern and western United States (Lack, Condor, 42, 1940:239–241; Phillips, Auk, 32,

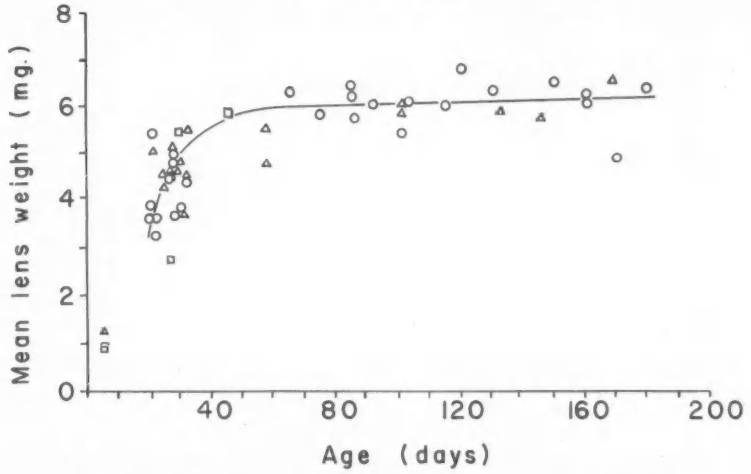

Fig. 1. Growth of eye lens (dry weight) in House Sparrows (*Passer domesticus*). Triangles represent males, circles represent females, and squares represent birds whose gonads were not seen.

1915:51–59). Likewise, no difference in lens growth rate was evident in this study between birds from Michigan and those from California. As eastern and western House Sparrows are so similar, the results of lens growth of birds from both states are presented together.

Nestlings were aged to the nearest day by comparison with Weaver's (Wilson Bull., 54, 1942:183–191) descriptions of nestling House Sparrows. Birds with incompletely ossified skulls were aged by comparing their ossification patterns to the series of ossification patterns of House Sparrows of known age up to 185 days drawn by Nero (Wilson Bull., 63, 1951:84–88). Because of the degree of individual variation in rate of skull ossification, ages of birds in the present work are accurate probably to within three days for birds younger than 35 days and to within 10 days for older birds. Sparrows with fully ossified skulls were grouped as adults. Eyes were preserved for at least a week in 10 per cent formalin. The hardened lenses were then cut loose from the eyes, cleaned by rinsing in water, and dried at about 60°C. in a drying oven for 24 hours or more before being weighed. No further decrease in weight occurred when lenses were dried for longer periods. Each lens was weighed on one of two chainomatic analytical balances or on a more convenient Roller-Smith precision balance.

The growth rate of the eye lens of House Sparrows during the first six months after hatching is shown in figure 1. Each point plotted on the graph represents the mean dry weight of the left

and right lenses of a single bird, except that 11 of these 51 points represent a single lens weight, as the contralateral lenses of these 11 were lost before they could be weighed. Lens weight increased noticeably in sparrows between the ages of six days (the youngest bird in the sample) and two months. Any increase that may have occurred in average lens weight after two months was insignificant compared with the difference between individuals. The average dry weight of the lens of 45 fully ossified, adult House Sparrows in milligrams was 6.170 ± 1.484, 95 per cent confidence limits. No difference in dry lens weight was apparent between males and females. When the data were tested by the t-test, the probability was greater than 0.50 that the mean lens weight of sparrows between two and six months of age was not significantly different from the mean lens weights of adults. These results show that lens weight is useless in aging House Sparrows older than two months.

The accuracy of the measurements as well as the reliability of the lens technique may be expressed by comparing weights of both lenses from the same bird. In 74 of the total of 96 birds, both the left and right lenses were weighed. One would expect the lenses from any one bird to have the same weight, but the left and right lenses differed in weight an average of 4.11 per cent of the mean dry weight of adult lenses, expressed in milligrams as 0.253 ± 0.059, 95 per cent confidence limits.

The lens technique appears to be of little use also in aging other species of birds. Dr. R. D. Lord (*in litt.*) found individual variation in lens weights to be so great that the lens technique was of no use in aging Ring-necked Pheasants (*Phasianus colchicus*). Howard Campbell (*in litt.*) found that Scaled Quail (*Callipepla squamata*) could not be separated by the lens technique in the fall into birds of the year and full adults. Miss Lois I. Bear (*in litt.*) also found overlap and little further increase in lens weight in Redwinged Blackbirds (*Agelaius phoeniceus*) by the time the birds had attained the age of the postjuvenal molt.

Although the eye lenses of cottontail rabbits continue to add significant lens material for nearly three years, the eye lenses of House Sparrows reach adult size when the birds are two months old. This difference in growth rate may be related to differences in the life histories of mammals and birds. Sparrows are fledged at an earlier age than that when rabbits leave the burrow, and they consequently have to possess well-developed sense organs to find food and avoid predators at an earlier age. In addition, birds in general are more dependent on a visual sense, whereas small mammals depend more on other sensory modes, such as smell and touch. The more rapid growth of the avian lens may be thought of as reflecting natural selection for early development of the eye as the sensory receptor for the primary sensory mode.

I would like to thank A. E. Aronoff, L. Case, H. Cogswell, F. B. Gill, J. P. Rood, M. Marsh, C. G. Thompson, and L. L. Wolf for helping me collect House Sparrows. For the use of equipment I am indebted to the University of Michigan Museum of Zoology, the University of Michigan Biological Station, and the Museum of Vertebrate Zoology. I am grateful to Dr. A. H. Miller, Dr. R. W. Storer, and Dr. H. B. Tordoff for their suggestions in the course of this work.—ROBERT B. PAYNE, *Museum of Vertebrate Zoology, Berkeley, California, January 26, 1960.*

Malaspina's Early California Ornithological Report.—Attention recently has been focused on the scientific investigation conducted at Monterey, California, in September, 1791, by Captain Alejandro Malaspina. The history of this investigation has been most interestingly and factually reported in a book by Donald C. Cutter, entitled "Malaspina in California," published by John Howell-Books, San Francisco, California, 1960.

Ornithologists will be especially interested in the section on Cardero's Birds of California. The only colored plates in the book are four paintings of birds done by the expedition's artist Jose Cardero. The author writes "Of the art emanating from California it is possible to identify definitely or provisionally some twelve items produced by ex-boatswain Jose Cardero." The four birds illustrated in color are the Redwinged Blackbird (*Agelaius phoeniceus*), the Red-shafted Flicker (*Colaptes cafer*), the California Thrasher (*Toxostoma redivivum*) and the California Quail. (*Lophortyx californicus*). This is the second known drawing of the state bird. The California Quail was first done in black and white by a member of the La Perouse group in September 1786. The third representation of the California Quail was done by a member of the Bodega Expedition of the Limits, about a year after Cardero's illustration.

This note is published to draw attention to an additional item in the bibliography of early California ornithology.—C. V. DUFF, *Los Angeles, California, February 4, 1961.*

Notes on a Colony of Forster Terns at Timnath Reservoir, Colorado.—A recent nesting of Forster Terns (*Sterna forsteri*) at Timnath Reservoir in northern Colorado is worthy of note, since there appears to be a detailed account of only one other nesting of the species in the state (Rockwell, Condor, 13, 1911:57). The rather grebe-like nesting described by Rockwell, at a site only 50 miles from Timnath Reservoir, is quite different from the one that I found.

On June 8, 1957, I saw large numbers of Forster Terns flying over Timnath Reservoir, a shallow, fluctuating irrigation reservoir in the rolling plains five miles east southeast of Fort Collins, about 4900 feet in elevation. After searching two small islands and the few little marshy patches around the lake's shore without finding any of their nests, I investigated the large, barren earth-bar, about 100 to 200 feet wide and several hundred yards long, which extends south into the reservoir from the northwest shore. There I found a sizable colony. There were 52 occupied nests and in a few nests the eggs had somehow been broken. The nests were placed on both the east and west edges of the south end of the bar, but there was none on the extreme tip.

The nests, unlike the bulky marsh nests described by Rockwell, were simply small, neatly-hollowed platforms of weed stems, scattered a few feet apart on the bare mud of the shores of the long peninsula, or on the small windrows of rubbish only a foot or two out in the water. With the exception of a single nest in the middle of the bar, almost all of the nests were within ten feet of the water and were only a few inches above it. The reservoir had been at capacity for some time. The nests also resembled those of avocets. In 23 of the nests there were three eggs, in 15 there were two, and in 12 only one. One nest held four eggs and another five; both of these nests possibly contained the eggs of two females. While I was examining the nests, the parent birds, accompanied by numbers of Black Terns (*Chlidonias niger*) and gulls from the nearby fields, were flying low overhead, screaming their harsh, low, rasping calls. A few boldly attacked me, swooping from a height of about 20 feet in very rapid diagonal dives, missing my head by a foot or two. When I left the colony the parents quickly began to settle back on the bar.

On June 11 I found most of the nests destroyed, apparently by predators. Of the 120 eggs originally in the colony, all but 25 were missing, broken or punctured. Of the 52 nests only 19 still contained any intact eggs, and some of these may have been deserted, as there were but few Forster Terns flying about.

On June 25 I found the colony to be entirely deserted, apparently without a single young tern having hatched. Only two Forster Terns were flying over the lake, and the large flocks of gulls and Black Terns had disappeared. In the three years since then I have not seen any attempt to re-establish nesting on Timnath Reservoir, although terns are still frequently noticed there.—Donald G. Davis, *Timnath, Colorado, December 15, 1960.*

Indigo Bunting at Carmel, California.—On February 1, 1959, at my banding station at Carmel Highlands, 4 miles south of Carmel, Monterey County, California, a bird was sighted which appeared to be of the genus *Passerina*. On February 2 the bird was trapped. From preliminary examination of the bird in hand it was believed to be either an Indigo Bunting (*Passerina cyanea*) or a Lazuli Bunting (*P. amoena*). Because of the difficulty of distinguishing these species in winter plumage, especially first-year birds, and because it was deemed unwise to band and release an inadequately identified bird, the bunting was kept in an aviary in order to be certain of its identity after the prenuptial molt, or if an immature, until the second prenuptial molt when full adult plumage would be expected.

By April, 1959, the bunting had acquired blue contour feathers, without the pectoral band of the male *amoena*, but with brown primary coverts, which indicated a first-year male *cyanea*.

Feeding and general aviary care were not difficult and the bird seemed in good health through its first postnuptial molt. On December 27, 1959, however, the bunting was found dead. It was deposited as a specimen (male, no. 141719) in the Museum of Vertebrate Zoology, where it was identified as *Passerina cyanea*. Wing and tail measurements (66.7 and 50.0 mm., respectively) fell within the range for *cyanea* and were below the minima for *amoena* (wing 70.61, tail 52.58) as given by Ridgway (The Birds of North and Middle America, Pt. 1, 1901:585).

Because of the occurrence of hybridization between *cyanea* and *amoena* (see Sibley, Auk, 76, 1959:443–463), and because of the instance recorded by Bleitz (Condor, 60, 1958:408) in Los Angeles

County, California, in 1956, in which a male Indigo Bunting was mated to a female Lazuli Bunting, special attention was given to the possibility that the present individual might be a hybrid from a similar cross breeding. It was the conclusion of John Davis and Ned K. Johnson, that there was no indication of such hybridization. There have been two other Indigo Buntings taken in California (see Bleitz, *op. cit.*), and there are three sight records made in the state, all from the San Francisco Bay area and all in 1939 (Grinnell and Miller, Pac. Coast Avif. No. 27, 1944:574).

I am indebted to both Davis and Johnson for comparing specimens in the collections at the Museum of Vertebrate Zoology and for confirming the identification.—LAIDLAW WILLIAMS, *Carmel, California, December 15, 1960.*

Dragonfly "Attacks" Hawaiian Hawk.—On the island of Hawaii on October 26, 1960, I was watching two Hawaiian Hawks or Ios (*Buteo solitarius*) circling about 300 feet overhead when I noticed a dragonfly make contact with one of them, rapidly back off about 20 feet, then dart in again to make contact. During the 5 minutes that the hawks were in sight, the dragonfly would dart in about every 15 seconds, make contact with the forepart of the wing or body of the hawk, dart quickly back, and keep a discreet distance until the next "attack." The dragonfly confined its attention to one hawk although at times the two were so close together that it appeared the dragonfly might easily have turned its attention to the other. The hawk appeared to ignore the whole episode.—EDWIN I. STEARNS, *Westfield, New Jersey, November 20, 1960.*

Pomarine Jaeger in Mount Rainier National Park.—On the morning of September 1, 1960, visibility was 40 to 50 miles in the Cascade Range of northwestern Washington with a heavy stratus cloud overcast at 14,000 to 15,000 feet. There had been rain and fog but no marked storms along the Washington coast in the preceding week and the winds were light and variable. About two inches of snow fell later in the day at 6500 feet on the east slope of the mountain.

At 9:30 a.m. at Panorama Point 6800 feet above sea level on the south slope of Mount Rainier, I watched a seabird skimming along the mountainside toward me several hundred yards to the northeast. As the bird approached, it was seen to be a large jaeger pursuing a steady course southwestward at about 6860 feet above sea level. It seemed to evince a sort of friendly curiosity by circling me once at a distance of about 50 feet. As it soared at right angles to my line of vision it was immediately recognizable by its elongated, round-tipped central tail feathers as a Pomarine Jaeger (*Stercorarius pomarinus*) in dark phase.

Park Naturalist V. R. Bender states that this is the first record of the Pomarine Jaeger in Mount Rainier National Park. This species has been considered accidental on inland waters of the Pacific states.—JAMES A. BRUCE, *Wooster, Ohio, December 3, 1960.*

Sparrow Hawk Feeding on Dragonflies.—In July and August, 1954, while employed on the Locke Ranch, Lockeford, California, I had several opportunities to observe an adult female Sparrow Hawk (*Falco sparverius*) feeding on dragonflies.

From a perch on a short dead branch of a felled tree the Sparrow Hawk would watch for passing insects. When a dragonfly passed the perch, the hawk would dart out, flycatcher-fashion, and attempt to overtake it. Upon overtaking the dragonfly, the hawk would tilt her body and attempt to strike the insect to the ground with her wing. She would then drop to the ground, seize the dragonfly, return to the log, and eat the dragonfly, discarding the head and the wings. Occasionally, this hawk made several passes at a dragonfly without capturing it.

On one occasion, I flushed the Sparrow Hawk off her perch and inspected the flat log surface she used as her feeding area. I found the head and wings of one libellulid and seven aeschnid dragonflies. I also found a single uneaten male acraea moth (*Estigmene acraea*).—LOUIS N. LOCKE, *Patuxent Wildlife Research Center, Laurel, Maryland, December 8, 1960.*

NOTES AND NEWS

Programs of divisional meetings of the Cooper Ornithological Society in early 1961 have included the following: John H. Kaufmann on "The Barro Colorado Biological Research Station, Panamá" at Berkeley on January 5; Ned K. Johnson on "Territorial Behavior and Vocalizations in Three Species of *Empidonax* Flycatchers" at Berkeley on February 2; William J. Hamilton III on "An Experimental Analysis of Bobolink Migration" at Berkeley on March 2; John B. Davidson on "An Australian Walkabout" at Los Angeles on January 25; Klaus Hoffmann of Wilhelmshaven, Germany, on "Sun Orientation in Birds and Other Animals" at Los Angeles on February 22; and Herbert Friedmann on "The Weaver Birds of Africa" at Los Angeles on April 26.

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the life sciences is September 15, 1961. Proposals received prior to that date will be reviewed at the fall meeting of the Foundation's advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the September 15, 1961, closing date will be reviewed following the spring closing date of January 15, 1962.

Inquiries should be addressed to the Biological and Medical Sciences Division, National Science Foundation, Washington 25, D.C.

At the thirty-second annual meeting of the Cooper Ornithological Society held in Tucson, Arizona, the following papers were presented on April 7:

Existence and Distribution of Native Passerines of Kauai, Hawaii, by Frank Richardson

The Effects of Restricted Food Consumption on the Nocturnal Activity (*Zugunruhe*) of Captive White-crowned Sparrows in the Spring, by James R. King and Donald S. Farner

The Isthmus of Tehuantepec and Cloud Forest Biogeography, by Byron E. Harrell

Distributional Patterns of Geographically Variable Birds in Utah, by William H. Behle

Ecological Studies of Hole-nesting Birds in British Columbia, by William D. McLaren

Attempts to Establish the Masked Bob-white in Arizona, by Lewis Wayne Walker

Nesting of the Alaska Jay at Anchorage, Alaska, by Leonard J. Peyton and Sidney B. Peyton

Interspecific Territoriality in Birds, by Ned K. Johnson

Specific Limits and Distribution of Ash-throated and Nutting Flycatchers, by Wesley E. Lanyon

Problems in Comparing Fossil and Recent Birds, by Dean Amadon

Observations on the Fossil Record of the Anatidae, by Hildegarde Howard

The Evolution of Form and Function of a Single Muscle in Birds, by William George

Morphologic Variation in Breeding White-crowned Sparrows of the Pacific Coast, by Richard C. Banks

A Consideration of the Taxonomic Position of the Genus *Anhinga*, by Oscar T. Owre

On April 8 the following papers were presented:

The Filoplumes of the White Leghorn Chicken, by Peter Stettenheim

The Effects of Certain Environmental and Biological Factors on Rally Calling in the Chukar Partridge, by H. Warrington Williams

Cliff Edge Responses in Gull Chicks, by John T. Emlen

Breeding Biology of the Red-tailed Tropic Bird, by Thomas R. Howell and George A. Bartholomew

Distinction and Distribution of Wintering Sandhill Crane Races in the Southwest, by John W. Aldrich, Thomas D. Burleigh, Erwin Boeker, William S. Huey

Breeding Cycles of Colombian Birds, by M. Dale Arvey

Seasonal Distribution of Breeding in an Equatorial Cloud Forest, by Alden H. Miller

Gonadal Influence on Vernal Premigratory Fattening, by Martin L. Morton

Lunar Influence on Migratory Restlessness in the White-crowned Sparrows, by L. Richard Mewaldt

Nest-building and Breeding Behavior by Castrate Weaverbirds, by Nicholas E. Collias, Donald S. Brooks, and Peter Frumkes

Water and Salt Economy of California Quail and Mourning Doves, by Richard E. McMillen and George A. Bartholomew

Bird Depredations in Arizona, by Floyd A. Thompson

COOPER ORNITHOLOGICAL SOCIETY, INC.
STATEMENT OF CASH RECEIPTS AND DISBURSEMENTS
FOR THE YEAR ENDED DECEMBER 31, 1960

CASH IN BANK, DECEMBER 31, 1959			$ 8,151.25
ADD: CASH RECEIPTS			
General Publication Fund			
Membership dues, regular and sustaining	$ 5,025.38		
Subscriptions for The Condor	962.35		
Condor sales	551.13		
Phonograph record sales (1 record sold)	7.50		
Dividends and interest received on endowment funds invested (Note A)	6,362.62		
Transfer from Avifauna Fund	1,000.00		
Contributions received for the publication of The Condor	1,065.00		
Other cash receipts	972.75	$15,946.73	
Avifauna Fund			
Avifauna sales, net (Note B)	$ 6,693.84		
Contributions received	7.00		
Other cash receipts	100.86	6,801.70	
Endowment Fund			
Life memberships and installment payments received on life memberships	$ 825.25		
Contributions received	11.00		
Other cash receipts	1,026.64	1,862.89	24,611.32
			32,762.57
DEDUCT: CASH DISBURSEMENTS			
General Publication Fund			
Publication Costs of The Condor			
Printing	$11,202.88		
Engraving	1,879.81	$13,082.69	
Cost of phonograph records		1.52	
Administrative Expenses			
Northern division	$ 92.47		
Southern division	138.93		
Annual meeting	1,089.56		
Business manager	378.24		
Accounting	150.00		
Treasurer	935.93		
Editor	899.88		
Other disbursements	288.26	3,973.27	
Avifauna Fund			
Sales tax paid	$ 7.82		
Printing and engraving	5,603.20		
Shipping and postage	293.63		
Transfer to General Publication Fund	1,000.00		
Other disbursements	1,185.71	8,090.36	
Endowment Fund			
Purchase of corporate securities		13.50	25,161.34
CASH IN BANK, DECEMBER 31, 1960			$ 7,601.23

CASH IN BANK ALLOCATED TO FUNDS AS FOLLOWS:	Dec. 31, 1959	Dec. 31, 1960
General Publication Fund	$ 1,520.43	$ 409.68
Avifauna Fund	5,794.18	4,505.52
Endowment Fund	836.64	2,686.03
TOTAL	$ 8,151.25	$ 7,601.23

Note A: At December 31, 1960, the business manager had in his custody endowment funds invested in corporate securities which cost $57,847.28, and had a market value of $178,997.13. This endowment fund includes contributions received in the names of Florence M. Bailey, Louis B. Bishop, Albert E. Colburn, Joseph Grinnell, A. Brazier Howell, and Harry R. Painton.

Note B: At December 31, 1960, the Society had a stock of Avifaunas for which the total of quoted list prices was $43,326.50.

C. V. DUFF, *Business Manager*

***For Sale, Exchange, and Want Column*—Each member of the Cooper Society is entitled to one short advertising notice in any issue of the Condor free. Notices of over 3 lines will be charged for at the rate of 25 cents per line. Send advertising copy to Jack C. von Bloeker, Jr., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.**

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WANTED—A copy of "The Ivory-billed Woodpecker" by James Taylor Tanner, Research Report No. 1, National Audubon Soc., N. Y., 1942.—J. G. SUTHARD, *1881 Raymond Ave., Long Beach 6, Calif.*

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POSITION WANTED—Museum Curator, young, married, with B.S. degree and some graduate work, desires position teaching biology, botany, or zoology in college, jr. college, or prep school. Some teaching experience; will work for advanced degree in summers.—W. M. SHAUGHNESSY, *Pennsylvania State Museum, Harrisburg, Pa.*

WANTED—Needed to complete my COS file: Bull. Cooper Ornith. Club, vol. 1, nos. 3, 4; The CONDOR, vol. 2, no. 6, and vol. 3, no. 2. Will buy any one, two, three, or all four items.—JACK C. VON BLOEKER, JR., *Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, Calif.*

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Articles published in the Condor normally are written by members of the Cooper Ornithological Society. Practically all the Society's money goes into the journal; neither the editor nor the business manager receives any pay other than the satisfaction of doing a service worthily. The preparation of good copy by the author will contribute greatly to accuracy of published output, dispatch in handling, and economy of production.

To be acceptable for inclusion in the Condor, articles should contain original material and indicate its significance. They must not duplicate in any substantial way material that is published elsewhere. Any type of subject bearing on birds will be considered. Manuscripts should be sent to the editor at the Museum of Vertebrate Zoology. Proofs with edited manuscripts will be sent to authors, at which time reprints may be ordered.

In the interests of accuracy and economy, observe the following: do not duplicate data in text, tables, or charts; check citations to original sources and verify text references; quoted statements must be exact replicas of the original; use vernacular names applicable to the entire avian species (for a guide in this regard, consult the A.O.U. Check-list of North American Birds, Fifth Edition, 1957); insert scientific names for species but not the subspecific name except in taxonomic papers or where the race concerned has been critically determined by the author or his collaborators on the basis of specimens; revise the manuscript repeatedly to remove superfluous words and phrases, immaterial detail, and repetitious statements.

Note Condor style and usage. "General Articles" and the "Field and Study" items are set up in different form. Provide a concise, meaningful title, and, where needed, subtitles within the text. Footnotes are not used. The address line may serve to indicate institutional connection, and to it should be added the date of transmittal of the manuscript. Terminal bibliographies are usually desirable where five or more titles are to be cited; otherwise, the references may be included in the text. For bibliographic style, note closely the practices employed in recent volumes of the journal. A factual summary is recommended for longer papers.

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Illustrations.—Photographs should be glossy prints of good contrast. Make line drawings with India ink; plan linework and lettering for at least ½ reduction; do not use typewritten labels on the face of the drawing. Provide typed legends on separate sheets.

Helpful references on writing: Manual of Style, University of Chicago Press, and Rules of the Editorial Committee, University of California Press. On scientific nomenclature: Fifth Edition of the A.O.U. Check-list, The Distribution of the Birds of California (Pac. Coast Avif. No. 27), and The Distributional Check-list of the Birds of México, Parts I and II (Pac. Coast Avif. Nos. 29 and 33); authors are not required to follow the nomenclature of these works.